ECOLOGY

Vol. 35 APRIL, 1954 No. 2

FOREWORD

This number of Ecology is dedicated as a Memorial to Dr. Frederic E. Clements in accordance with the motion adopted by the Ecological Society of America in its annual meeting on September 9, 1952. The first part of this number is a supplement to the regular issue and consists of nine invited articles as a special honor to Dr. Clements. The cost of publishing these special papers was paid for by contributions from members of the Society and others (listed in the June, 1954, number of the Bulletin of the Ecological Society of America) and by receipts from advertisements.

"Man will never be master of his environment and hence of his destiny until he understands the universal ebb and flow of processes and compels these to his own advantage. Though the great earth movements and shifts of climate are beyond his control, the ultimate consequences in terms of rain and drouth, erosion and flooding, security or disaster are in his hands if he has but the wit to command them."—Frederic E. Clements. 1936. Environment and life in the Great Plains.

The Frederic E. Clements Memorial Committee:

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Frederic Edward Clements

1874-1945

FREDERIC EDWARD CLEMENTS

RAYMOND J. POOL
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Well do I recall the day in the early summer of 1904 when I first met Dr. Fred Clements. Our class in high school botany had learned of him from a guide for laboratory work which he had published. That summer day when Clements stepped from the local train in a small Nebraska town, we were on the platform to greet him. He and his wife were on their way to attend the Louisiana Purchase Exposition which was then in progress in St. Louis. It was thus that we met Dr. Frederic Edward Clements very early in the half-century during which he forged an amazing career as one of the world's outstanding figures in the general field of biology and in the rapidly evolving specialty of plant ecology. He was an unusually bold, brilliant pioneer as he set out to help to formulate the fabric and to mould the trend of American thought in teaching and research in plant ecology.

Clements entered the field of ecology at an opportune time and place. He was born September 16, 1874 in the shadow of the young University of Nebraska, which itself was only five years of age. The University was in the pioneer village of Lincoln, then less than ten years old, and in an area that had achieved statehood only seven years previously. Famous Indian battles were yet to be fought across the rolling grassland frontiers. The broad Nebraska prairies were largely yet to feel the plough. The stage was ready for the coming of the men of science who eventually were to make the flora and the natural vegetation of the vast Prairie Province of North America the best known and the most intimately known of all the world's great grasslands.

Young Clements entered the University of Nebraska when he was but sixteen. There he earned the B.Sc. degree in 1894, the A.M., in 1896, and the Ph.D., in 1898, the latter for outstanding work in phytogeography. His alma mater conferred the degree of LL.D. upon him in 1940. His thesis for the master's degree was entitled: "The Histogenesis of the Caryophyllales," and for the doctor's degree the thesis was on: "The Phytogeography of Nebraska." The latter work was published with Roscoe Pound as joint author. The two theses were early indicators of Clements' expanding interests in the fields of morphology, taxonomy, phylogeny, and ecology that were to characterize his entire life.

Dr. Clements served on the faculty of the Department of Botany at the University of Nebraska from the time he was appointed a laboratory assistant in 1894 until he resigned as a full professor in 1907. The latter year he accepted the position as Professor of Botany and Head of the Department of Botany at the University of Minnesota. He left Minnesota in 1917 to become a Research Associate in Ecology with the Carnegie Institution of Washington, D. C., a position to which he devoted the rest of his life. He and his wife, who for many years was his assistant and illustrator, lived in Tucson, Arizona until 1925 when they moved to Santa Barbara, California. During these years the Clementses maintained an interesting Alpine Laboratory on Pikes Peak in summer and, after the move to California, he also assumed the supervision of the work at the Coastal Laboratory of the Carnegie Institution at Santa Barbara during the winter months. During these many years of uninterrupted research, Clements familiarized himself with the vegetation of North America with a thoroughness that has never been surpassed.

Clements was a member of numerous state, national, and international scientific and professional organizations and societies. He served on International and American Nomenclature Commissions in 1905 and 1902 respectively. Member, British Ecological Society; Societas Phytogeographica Suecana; Real Academia Agricoltura Italiana; International Congress of Science, Secretary 1903. He became a member of the A.A.A.S. in 1896, elected Fellow in 1898, Councillor 1905 and 1909, and General Secretary 1910; Botanical Society of America 1898, Vice-President 1905, Councillor 1906-1910; Mycological Society of America, Secretary 1903; Society of American Naturalists, Director 1905; American Microscopical Society 1897; American Geographic Society 1900; American Breeders Association 1908; Ecological Society of America; Director, International Phytogeographical Excursion in America, 1913; Associate Editor, Mycologia 1907; American Society of Plant Physiologists; American Society of Mammalogists; Society of American Foresters; Paleontological Society of America; American Meteorological Society.

During his undergraduate and graduate years at Nebraska, he was a leader of scientific and

cultural organizations and was elected to Phi Beta Kappa and Sigma Xi. He served in official capacities in the latter societies, as well as in the Nebraska and Minnesota Academies of Science. He was an idealist of the highest type and his brilliance of mind and broad interest in many fields of science, history, politics, and society made him a sparkling conversationalist and companion. His approaches to the teaching profession, and to ecological research, were characterized by a boldness and originality which approached the iconoclastic at times.

A feature of Clements' early education, training, and experience that is not widely known was the depth and breadth of the foundation he laid for his career. He was doing extensive and intensive work in the field and laboratory on the taxonomy of the flowering plants and fungi and in phytogeography while still an undergraduate. He was a responsible assistant in the Department of Botany at a very early age. He had also taken much work in modern language and literature and in the classics. His thorough training in language was to prove a very valuable asset as, in later years, he endeavored to build a properly formed and meaningful set of scientific terms which the growing field of ecology badly needed. His sincere and constant effort to formulate and to stabilize a sensible, workable, and much-needed terminolgy for ecology was soon to mark him and in later decades to make him widely known.

At the beginning of the century, there were not a half-dozen ecologists in the whole world. When the "Phytogeography of Nebraska" was published there had been few serious attempts by anyone anywhere to analyze the structure and evolution of the vegetation of the world or any small part of it except in the most general way. There were then but a few observational phytogeographers even in the Old World. No one had yet subjected American habitats to a detailed analysis as to their origin, flora, structure, or life history as might be determined by ecological procedures. There were few or no instruments then available for such research and no one had set up acceptable methods for such investigations. The time was certainly ripe for the introduction and evolution of research methods in ecology. The development of a distinctive language by which ecologists could explain their especial interests and their findings to others was an imperative need.

The methods of ecological research and the ecological terminology that were evolved by Clements have been debated for a half-century. This is not the place to review this interesting phase of the history of plant ecology. The subject has been argued and reargued throughout the world wherever ecologists have gathered. Much of the critical attitude on this matter has stemmed from rather small sources when comparative background and practical experience are considered. It is perhaps appropriate and sufficient at this point to state an old maxim that the "proof of the pudding is in the eating thereof."

When one observes that the Clementsian principles of dynamic ecology, and, yes, much of the Clementsian brand of ecological terminology, have for a long time been thoroughly tested and used in scores of intensive and extended researches on vegetation throughout the world, one may conclude that the "pudding" must have been pretty good. The writer of this brief *vita* has frequently noted the adoption of various Clementsian features of ecology in the research programs and publications of such significant fields as forestry, grazing management, soil conservation, general agriculture, and even in zoology. This has been all the more amazing to one who knew Clements as a man with little or no original background in scientific or practical agriculture. The jargon and point-of-view of the farmer, the forester, the rancher and stock grower were mastered by Clements long after he had formulated his ecological philosophy and developed his principles and practices. One of his greatest pleasures in later life was to follow the success of the various agricultural projects and other practical researches which had utilized the procedures that his own endeavors had established. A leading European ecologist has fittingly stated that: "I am sure that Clements is by far the greatest individual creator of the modern science of vegetation and that history will say so."

Dr. Clements passed away in Santa Barbara, California, July 26, 1945, without issue. His devoted wife, Dr. Edith S. Clements, widely known for her excellent work as a botanical draftsman and author, lives at present in La Jolla, California.

Publications

This is a selection of the published papers and books of F. E. Clements, not a complete bibliography. Books are indicated by an *.

1893. New and noteworthy Nebraska plants. Rept. Bot. Surv. Nebr.

New species of fungi for Nebraska. Rept. Bot. Surv. Nebr.

1894. Bacteriaceae, Saprolegniaceae, Peronosporaceae. Rept. Bot. Surv. Nebr.

Botanical expeditions in Nebraska. Rept. Bot. Surv. Nebr.

New species of fungi. Rept. Bot. Surv. Nebr.

Additions to the reported flora of Nebraska. Rept. Bot. Surv. Nebr.

1896. New species of fungi. Rept. Bot. Surv. Nebr.

Additions to the reported flora of Nebraska. Rept. Bot. Surv. Nebr.

1897. Rearrangement of the North American Hyphomycetes. Minn. Bot. Stud.

Peculiar zonal formations of the Great Plains. Amer. Nat.

The polyphyletic disposition of the lichens. Amer. Nat.

1898. Zonal distribution and constitution of formations. Rept. Brit. Assn.

The phytogeography of Nebraska.* With Roscoe Pound.

The vegetation regions of the Prairie Province. Bot. Gaz.

1899. Histogenesis of the Caryophyllales. Trans. Amer. Micro. Soc.

1900. The teaching of high school botany. Nebr. Teacher.

Laboratory manual of high school botany.* With I. S. Cutter.

1901. The phytogeography of Nebraska.* Second edition.

New genera and species of fungi. Rept. Bot. Surv. Nebr.

Additions to the reported flora of Nebraska. Rept. Bot. Surv. Nebr.

1902. A system of nomenclature for phytogeography. Bot. Jahrb.

Greek and Latin in biological nomenclature. Univ. Nebr. Stud.

Herbaria Formationum Coloradensium. With E. S. Clements.

1903. Nova Ascomycetum Speciesque. Bull. Torr. Bot. Club.

1904. Development and structure of vegetation. Rept. Bot. Surv. Nebr.

Formation and succession herbaria. Univ. Nebr. Stud.

Plant geography. In Encyclopedia Americana.

1905. Research methods in ecology.* Univ. Pub. Co.

1906. Cryptogamae Formationum Coloradensium. Exsiccati, I, II.

1907. The real factors in acclimatization. Proc. Int. Hort. Cong.

The causes of winterkilling. Rept. Nebr. Hort. Soc.

The causes of alpine dwarfing. Science N. S.

Cryptogamae Formationum Coloradensium. Exsiccati, III, IV.

Plant physiology and ecology.* Holt.

1908. The ecologic view of the species concept. Amer. Nat.

Cryptogamae Formationum Coloradensium. Exsiccati, V, VI.

Guide to the spring flowers of Minnesota. With C. O. Rosendahl and F. K. Butters. Minn. Plant Stud. I.

Guide to the trees and shrubs of Minnesota. With C. O. Rosendhal and F. K. Butters. Minn. Plant Stud. II.

1909. Life-history of lodgepole burn forests. Bull. U. S. For. Serv.

Darwin's influence upon plant geography and ecology. Amer. Nat.

Plant formations and forest types. Proc. Soc. Amer. For.

Novae Species Ascomycetum Coloradensium Generaque. Minn. Bot. Stud.

A new genus of bluegreen algae. Minn. Bot. Stud.

The general of fungi.* Wilson.

1910. Minnesota mushrooms.* Illustrated by E. S. Clements.

A classification and use survey of Minnesota resources. Rept. Cons. Cong.

1911. Guide to the autumn flowers of Minnesota. With C. O. Rosendahl and F. K. Butters. Minn. Plant Stud.

Proposals for a system of tree breeding. Amer. Breeders Assn.

1912. Minnesota trees and shrubs.* With C. O. Rosendahl and F. K. Butters.

1913. Rocky Mountain flowers.* With E. S. Clements. Wilson.

1914. Herbaria Ecadium Californiae. Exsiccati. With E. S. Clements.

1916. Plant succession.* Carnegie Inst. Wash.

1917. Development and structure of the biome. Bull. Ecol. Soc. Amer.

1918. Scope and significance of paleo-ecology. Bull. Geol. Soc. Amer.

1920. Plant indicators.* Carnegie Inst. Wash.

1921. Aeration and air content.* Carnegie Inst. Wash.

Drought periods and climatic cycles. Ecology.

1923. The phylogenetic method.* Carnegie Inst. Wash. With H. M. Hall.

The ecological method in teaching botany. New Phytologist.

The nature of the problem of the cycle. Geog. Rev.

Experimental pollination.* Carnegie Inst. Wash. With F. Long.

1924. Experimental vegetation.* Carnegie Inst. Wash. With J. E. Weaver.

1926. The condition and needs of systematic mycology. Science N S. With C. L. Shear.

1927. The family tree of flowers. Natl. Geog. Mag. With E. S. Clements.

1928. Flower families and ancestors.* With E. S. Clements. Wilson.

1929. Experimental methods in adaptation and morphogeny. Jour. Ecology.

Climatic cycles and changes in vegetation. Geog. Rev.

Plant competition.* Carnegie Inst. Wash. With J. E. Weaver and H. C. Hanson.

Plant ecology.* With J. E. Weaver, 1929. Second Ed., 1938, McGraw-Hill; Spanish Ed., Acme Agency, 1944.

1930. The seven lean years. Outdoor Amer.

1931. The genera of fungi.* With C. L. Shear, Illustrated by E. S. Clements. Wilson.

1932. The method of collodion films for stomata. Carnegie Inst. Wash. With F. Long.

1933. Symposium on climatic cycles. Proc. Natl. Acad. Sci.

Competition in plant societies. Carnegie Inst. Wash.

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Effect of soil temperature on transpiration in *Helianthus annuus*. Plant Phys. With Martin.

1935. Elongation and expansion in *Helianthus* phytometers. Plant Phys. With F. Long.

Relict method in dynamic ecology. Jour. Ecology.

Social origins and processes among plants. Carnegie Inst. Wash.

Experimental ecology in the public service. Ecology.

Plant succession and human problems. Carnegie Inst. Wash.

1936. The origin of the desert climax and climate. Univ. Calif. Press.

Nature and structure of the climax. Jour. Ecology.

1937. Environment and life in the Great Plains. Carnegie Inst. Wash. With R. W. Chaney.

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1939. Bio-ecology.* With V. E. Shelford. Wiley.

1942. Cycles and climaxes. Chron. Bot.

FREDERIC E. CLEMENTS AS I KNEW HIM

ROSCOE POUND
Law School, Harvard University, Cambridge, Massachusetts

As a man, Frederic E. Clements was thoroughly conscientious, possessed of high ideals, and devoutly religious. He was tirelessly diligent, full of enthusiasm, very cooperative, and of good judgment. Also he showed the highest good taste in appearance and in all that he said and did. To all this I can testify with assurance from close association with him for more than a dozen years. I first saw him when, as a small boy, he used to deliver the morning paper. Later I saw him on the "scrub team" at football practice. But I did not become really acquainted with him till as a sophomore at the University of Nebraska he became a worker in the Botanical Survey of Nebraksa of which I was then Director.

It was my privilege to see him grow up as a botanist. As an undergraduate, he found himself in an atmosphere of great botanical activity especially in field work. Dr. Charles E. Bessey came to the University of Nebraska as Professor of Botany in the school year 1884-1885 and quickly attracted an enthusiastic group of students. In the school year 1885-1886, a group of seven began to work in the field together and to hold weekly meetings to read and discuss papers. This was the beginning of what became in 1887-1888 well-organized as the "Sem. Bot." Of those of the seven who went on in botany were J. G. Smith and myself of the class of '88, Herbert Webber of the class of '89, and A. F. Woods of the class of '90. I was Profesor Bessey's assistant in the school year 1888-1889, Webber held the place in 1889-1890, and Woods for some years after 1890-1891. In the school year 1891-1892, Smith and I started the Botanical Survey of Nebraska and the Flora of Nebraska. In July and August of 1892, Smith and I went through the sand-hill region of Nebraska on foot with a pack horse for supplies and instruments. We published at our own expense Part II of the Botanical Survey of Nebraska, Flora of the Sand-Hill Region, in April, 1893. After 1891, the "Sem. Bot." took in a number of graduate students of whom I remember particularly Rydberg, Saunders, and Shear, and work on the Botanical Survey and the Flora of Nebraska went on actively and continuously. Some or all of us went over substantially every part of the state collecting and observing.

As a freshman, Clements came into this active and enthusiastic botanical center in the school year 1890-1891 and took his degree of B.Sc. in June, 1894. In 1891, when he was a sophomore,

Woods and I were attracted by his zeal, ability and diligence. We devised a grade of "Cand." (I suppose *Candidatus*) for him and later promoted him to "Nov." (I suppose *Novitius*), and he entered actively into the work of the Botanical Survey and the Flora of Nebraska.

In 1895, I read Drude's "Pflanzengeographie von Deutschland" and published a review under the title "The Plant-Geography of Germany" in the *American Naturalist* for June, 1896. Clements and I had begun working together in that year after he succeeded Woods as Professor Bessey's assistant and we wrote together the portion of Part 4 of the Botanical Survey of Nebraska which had to do with the Fungi. This was published in January, 1896. At the time, after reading Drude's book, I got the idea of a Phytogeography of Nebraska. Clements took up the idea with enthusiasm and we worked upon it together at night (we were both busy in the daytime) for two years, publishing the first edition of our Phytogeography of Nebraska in 1898. We worked together on Fungi, on the Botanical Survey, and as editors and, in part, writers of the Flora of Nebraska until in 1901 pressure of professional work compelled me to give up regular activity in Botany. In particular, I remember how we worked out together by trial and error in the field the "quadrat method" described in our paper "A Method of Determining the Abundance of Secondary Species," published in *Minnesota Botanical Studies*, Vol. 2, June, 1898. This method he developed later into a more practical procedure. Besides the Phytogeography, we wrote together and published some seven papers between 1896 and 1898.

As we worked together, he told me he felt the need of linguistic training. The scientific curriculum had little place for languages beyond a small secondary school requirement of Latin. With characteristic energy, diligence, and determination he set to work to remedy the deficiency by self-teaching. I know the progress he made in Greek, reflected in his "Greek and Latin in Botanical Nomenclature" in 1902, and of his acquired ability to read in many languages. He even got a reading knowledge of Polish in order to be able to use Rostafinski's authoritative book on the slime-molds.

After 1894, Clements took the lead in the "Sem. Bot." and made it what it finally became. His great work was done in ecology after 1901 when I could no longer work with him and I know of it only from such botanical reading as I have been able to do in intervals of leisure. In 1907, he went to Minnesota as Professor and I to Northwestern as Professor of Law and to my great regret our paths parted.

Of his work in ecology, others are better qualified to speak than I who have been out of botany for fifty-two years. But as I read his writings after 1904 it seemed to me that he was increasingly developing a biological philosophy. I remember how he and I used to discuss Linnaeus' "Philosophia Botanica," a wholly unphilosophical book as we use the term philosophy today, and Spencer's "Principles of Biology" of which we had expected great things in the days when Comtian Spencerian positivism was almost a religion to scientists. Professor Bessey warned us that we would get nothing out of the book, but we read and discussed it only to find he was right. Our discussions during the controversy between the Darwinians and the Lamarckians at the beginning of the present century were more fruitful. Science has outgrown her philosophers. But Clements had an eminently philosophical mind.

The days of his work on the Botancial Survey of Nebraska were those of low salaries and meagre, if any, appropriations for research, field work, and printing. Much of the expense came out of our own pockets, which were empty enough. Much had to be begged from scientifically minded donors. Clements never grumbled, never became discouraged, never gave up. He went ahead uncomplainingly doing the best he could with what was available.

He played football in high school and, as I have said, on the "scrub team" in college. He rose to be an officer in the Cadet Battalion. He could and did walk a steady three and one-half miles an hour for hours at a time in the field. But I have suspected that this was largely a conscientious application of his will more than an exhibition of exceptional physical strength. His bodily strength was fortified by great strength of will.

A TRIBUTE TO FREDERIC E. CLEMENTS AND HIS CONCEPTS IN ECOLOGY

JOHN PHILLIPS
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As an ecologist outside the United States I am privileged indeed to contribute a few thoughts in honour of the outstanding ecologist of his time and generation, Frederic E. Clements.

While a student at Edinburgh in the years immediately after the Great War, I was so inspired by the famous "Plant Succession" that I, a brash undergraduate greatly daring, wrote to Clements about his concepts of succession and development. Back came a message of explanation and encouragement and the gift of reprints; thus was born in 1920 a correspondence and a bond of understanding that lasted a quarter of a century.

On my appointment in 1922 to a research post in the Forest Dept. of South Africa I initiated ecological study of the development and the sylviculture of the sub-tropical evergreen forests in the Knysna region. Here, during five wonderful years, I could consider the relevance and the application of Clements' views on succession, development, the biotic community, the climax, plant indicators and other subjects. Bews, the notable ecologist in Natal, had from 1912 onwards applied some of Clements' concepts in grassland and forest deevlopment. Accordingly, there grew up between him and me a link that went to strengthen my bond with Clements himself.

I remember Bews telling me in 1922 how long it had taken to get several highly distinguished South African botanists to believe in "this new fangled" plant succession. While not accepting all of Clements' views, Bews certainly made good use of certain of them, unquestionably finding them of value in clarifying the originally cloudy picture of ecological relationships in the wealth of the vegetation of Natal and Zululand. On leaving Knysna in late 1927, I found myself a staunch supporter of the Clementsian approach to development and the climax.

In Tanganyika came a splendid chance of considering in a totally new flora, with which is integrated a great game and other fauna, the relevance of the principles I had found applicable wholly or in part for the macchia and forest of midland South Africa. In the varied and extensive savanna as well as in the tropical and subtropical evergreen forests I again found a corroboration of much that I had noted elsewhere, but here I had scope for learning much more about the biotic community, in that I was initiating, in collaboration with C. F. M. Swynnerton, an ecological study of that complex biological problem, tsetse-fly (*Glossina* spp.) and its control. Habitat, vegetation, game and other forms of animal life and the vector of the trypanosome responsible for human and animal trypanosomiasis (sleeping sickness and nagana) provided a series of relationships requiring analysis, interpretation and the synoptic view of the ecologist.

On being appointed to the Professorship of Botany at the University of Witwatersrand, Johannesburg, in 1931, it fell to me to organise ecological and management studies into grassland of the Highveld and to investigate the ecological setting of a range of Bushveld (tree-and-grass savanna) types in the Transvaal. With the encouragement of the late General Smuts, Dr. Pole Evans, the then Director of the Botanical Survey, and others, I had, up to 1948, opportunity of testing ecological methods and principles over a wide range of country and conditions. Of particular significance was the privilege of helping to educate and train many workers in ecology, pasture management, soil conservation and related subjects: men and some women who had an ecological background and flair, and who today are widely spread over the continent of Africa. The work done and the investigations of students of an earlier day, who later undertook some form or other of ecological study, have gone to support the view that *mutatis mutandis* the broad principles of development and the community attributable to Clements, find application over a wide range of climates, vegetation types and related conditions. During this period I met Frederic Clements and his helpmeet, Dr. Edith Clements, in the United States. As an outcome of extensive travelling with them I was able to check many points in our working concepts. Some years later a research student of mine, R. Rose-Innes, had a similar experience. As an outcome of these personal contacts, we were able to clarify with Clements and certain of his senior colleagues various points of mutual interest. It is a pleasure to record that research and training in *bio-ecology* con-

tinues at Witwatersrand in the hands of several former students.

On accepting an invitation to help organise, on the agricultural side, what remained of the original East African Groundnuts Scheme, I had the chance of once more seeing something of my earlier love, Tanganyika. Here, during 1948-51, opportunity presented itself of setting in motion extensive ecological land-use surveys, most of the men responsible for the field investigations being old students of mine. On the fruits of these surveys, it was ultimately possible to base a wiser approach to the establishment of the Scheme on a pilot basis. Much was learned of method and factual nature by the survey teams. I myself left Tanganyika with a further need of information in support of the general principles of the Clementsian school.

Since 1951, service on International Bank Missions to Ceylon and Nicaragua and my taking up the task of establishing a Faculty of Agriculture in the Gold Coast, British West Africa, have enabled me to see a further range of climates and vegetation, and have also permitted me to renew my student-day acquaintance with European vegetation. All of this has helped to raise my valuation of the extensive range of application of the Clementsian views on the dynamics of vegetation.

Lest it be thought that this statement of a much varied set of experiences, in various parts of Africa and in several countries in three other continents, is tantamount to an avowal of an unquestioning acceptance of all that Clements wrote, I must emphasize that on a number of points he and I differed strongly, both in our years of correspondence and during the months of our single meeting. Tansley, in this journal, in 1935 (16: 284-307), in a kindly manner, hinted that my papers in the Journal of Ecology (1934-35; 22 and 23) on succession, development, the climax and the complex organism suggested a tendency to absorb the pure milk of the Clementsian word. I still hope to publish a corrective to my old friend's courteous but incorrect assessment, but suffice it to say that in the following major matters Frederic Clements and I agreed to differ:—

i) I have been for a long time prepared to accept that, under certain conditions of climate and soil, the influence of edaphic factors on development and the nature of the climax is paramount.

ii) In many respects I have been unable to agree that Clements'-views on the significance of much of what he considered *post-climax* relicts were indeed justified. Too much weight in his mental reconstruction of vegetation, to my mind, was placed upon the occurrence of such relicts.

iii) Although I had early attempted some elementary investigation of phytometers at Knysna (1925-27) and by means of research student collaboration later at Johannesburg (1932-37), I gradually found myself in marked disagreement with the author of the concept of the phytometer as to its real value as a means of measurement of the habitat.

iv) I thought his terminology at times unnecessarily rich, despite its classic correctness and the sharpness of definition he gave it. In fairness I must say that he was always prepared to consider points put to him, even if he did not always accept the suggestion made.

Remembering, by contrast, the overwhelming weight of argument in support of Clements' general concepts of succession, development, the climax and the complex organism as seen by my students and myself, I do not put too much stress on these points of difference.

From my talks with General Smuts, over the period 1931 to 1948, I know that soldier, statesman and philosopher found in the essence of Frederic Clements' ecological concepts appropriate food and apt bases for his philosophy of holism. Smuts particularly appreciated the philosophical soundness of the Clements concept of the biotic community and the complex organism.

Although I have dealt mainly with the basic significance of Clements' view and work, I must emphasize the remarkably wide application his concepts have had in all forms of practical study in various parts of the world, as for example in crop production, pasture or range management, soil conservation and forestry.

Frederic Clements lives on in the mind of a great host of students of pure and applied ecology in many lands: his thoughts will echo down the passages of time.

THE FREDERIC E. CLEMENTS MEMORIAL

VERNON A. YOUNG
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In the fall of 1951, Mrs. Edith S. Clements approved the establishment in the Range and Forestry Department of the Agricultural and Mechanical College of Texas of a Memorial in honor of her late husband, Dr. Frederic E. Clements.

The purpose of the Memorial is two-fold:

(1) It will serve as a depository for many of Dr. Clements' publications, partially prepared manuscripts, field notes and maps, numerous negatives and photographs of biological scenes and topics, and lantern slides representing ecological scenes of wide distribution throughout North America and certain regions of the Pacific Islands. In addition, it will house a large assortment of microscope slides dealing with various tissues of plants representative of a wide range of different environmental conditions and several relic tools and equipment pieces representative of the different periods in which Dr. Clements worked for approximately one-half century.

(2) The establishment of a scholarship fund by Mrs. Clements for worthy undergraduate or graduate students interested in the application of ecology to conservation or certain phases of dynamic bio-ecology. Mrs. Clements after years of field experience with her late husband recognized the increasing importance that ecology should assume in the conservation of our natural resources. Thus, the establishment of the scholarship will be both admirable and timely.

The first purpose is already being accomplished through shipments to the Range and Forestry Department of materials which Mrs. Clements has classified as desirable for the depository. As the materials are received, they are further classified, recorded, and placed in suitable subject matter containers and positions in the temporary exhibit room. When all the materials available are assembled, they will be permanently exhibited in a room of sufficient size to allow all to be seen or located with ease. Practically all these materials may be observed or studied in the room by interested faculty and student members.

Those interested in the detailed or general information of the various phases of ecology in North America will find Dr. Clements' papers, field notes, photographs, and other offerings to be particularly informative, as well as very important in leading the way into important research problems. It is this phase of the Memorial that should be important to the ecological field since Dr. Clements left a valuable collection of notes dealing with field problems, many of which only his keen analytical mind would recognize. Many of these notes may be very valuable in delineating definite ecological changes that have occurred in certain habitats over the areas he investigated for a period of more than fifty years. These field problems could, no doubt, be adequately handled today as research projects by graduates students who are trained in ecological fundamentals.

The second purpose of the Memorial to establish a scholarship will become available at a later date and will add much needed assistance to a comparatively new field. Although large sums of money are being made available through scholarships and research fellowships for capable young students interested in doing research in numerous scientific fields, only very limited amounts of money are available for students interested in the bontanical field and especially ecological research. Today the conservation of our precious soil and water resources of the nation depends largely upon what role will be played by our biological scientists in the field of dynamic ecology.

NATURE AND PLACE OF TRANSITION FROM TRUE PRAIRIE TO MIXED PRAIRIE

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As a memorial to Dr. Frederic E. Clements, it is a pleasure to present this paper on the mid-continental grasslands of North America. Born and reared at Lincoln, Nebraska, he developed a remarkable interest in and love for the prairie. He has often stated to the first author that of all the vegetation of North America, he liked the grassland best. Clements was the first to recognize the Mixed Prairie as a distinct plant association and to describe its nature and range and the grouping of the dominants (1920).

When one examines the prairies of western Iowa and then proceeds some distance westward, he is impressed by several changes. The vegetation is reduced in height, it becomes less dense, and takes on a distinctly more xeric impress. These changes result from gradually increasing unfavorable water relations as the vegetation of True Prairie gives way to that of Mixed Prairie. Along the Nebraska-Kansas interstate line, for example, the 33-inch annual precipitation near the Missouri River decreases westward at an average rate of about an inch every 15 miles. Conversely, rate of evaporation rapidly increases.

In Nebraska, the transition from True to Mixed Prairie occurs over three types of topography. South of the Platte Valley Lowland it has been traced over the nearly level portion of the Loess Plain Region (Fig.1). Northward, the transition takes place in the greatly dissected Loess Hills and Plains. East of the northern Sandhill Region, it occurs on the Holt-Pierce Plain and Boyd Shale Plain.

Transition in the Loess Plain Region

In an extensive study of prairie (Weaver and Fitzpatrick 1934), a large number of stations were selected extending from Belleville, Kansas, in Republic County, through the tier of counties lying due northward to Yankton County in South Dakota (Fig. 2). The vegetation at each of these stations was found to be True Prairie. Another lot of stations about 30 miles westward, extending from Mankato in Jewel County, Kansas, northward through Nuckolls, Clay and Hamilton Counties a few miles west of the 98th meridian to the Platte River, was found to represent an area in which transition to Mixed Prairie was clearly beginning. Approximately 70 miles westward, studies were made at Phillipsburg in 1920-1923 (Clements and Weaver 1924), and at Hays, Kansas, from 1930-1935 (Albertson 1937). Later studies were extended northward through Alma and Holdrege, Nebraska (Fig. 2). These investigations showed clearly that here typical Mixed Prairie prevailed. Extensive study of the intervening area, about 50 miles in width, has confirmed that it is here that the transition occurs.

Changes Accompanying the Transition

Difference in the more mesic prairies of Iowa and Missouri from the more xeric ones westward have been pointed out by Weaver and Fitzpatrick (1934). Height growth in groups of prairies in one area was compared with that of groups in other areas during the same season. For example, in northeastern Kansas and southeastern Nebraska, average height of little bluestem (*Andropogon scoparius*)[1] on July 12, 1929, was 13 to 18 inches, which was 5 to 8 inches greater than near Lincoln, Nebraska, five days later. Height growth of foliage of big bluestem (*A. gerardi*) in three prairies in southeastern Nebraska and Iowa was 21 to 33 inches on August 28-30. This was 8 to 9 inches greater than that at three stations near Lincoln, during August and September. During July 7-12, 1931, little bluestem averaged 7 to 12 inches tall at a group of five stations in southern Nebraska and northern Kansas near the western border of True Prairie. A week later measurements at five stations in west-central Iowa gave averages which were twice as great.

As one proceeded westward toward the transition region the grass became shorter and more mesic species did not extend so far up the slopes. For example, at stations 80 to 110 miles west of the Missouri River, little bluestem was 12 to 14 inches tall on June 26, 1931. But 25 to 35 miles farther west, the height was only 9 to 12 inches two weeks later. Similarly, big bluestem was 15

[1] Nomenclature of grasses follows Hitchcock and Chase (1950); that of other species is according to Britton and Brown (1913) unless other authority is given.

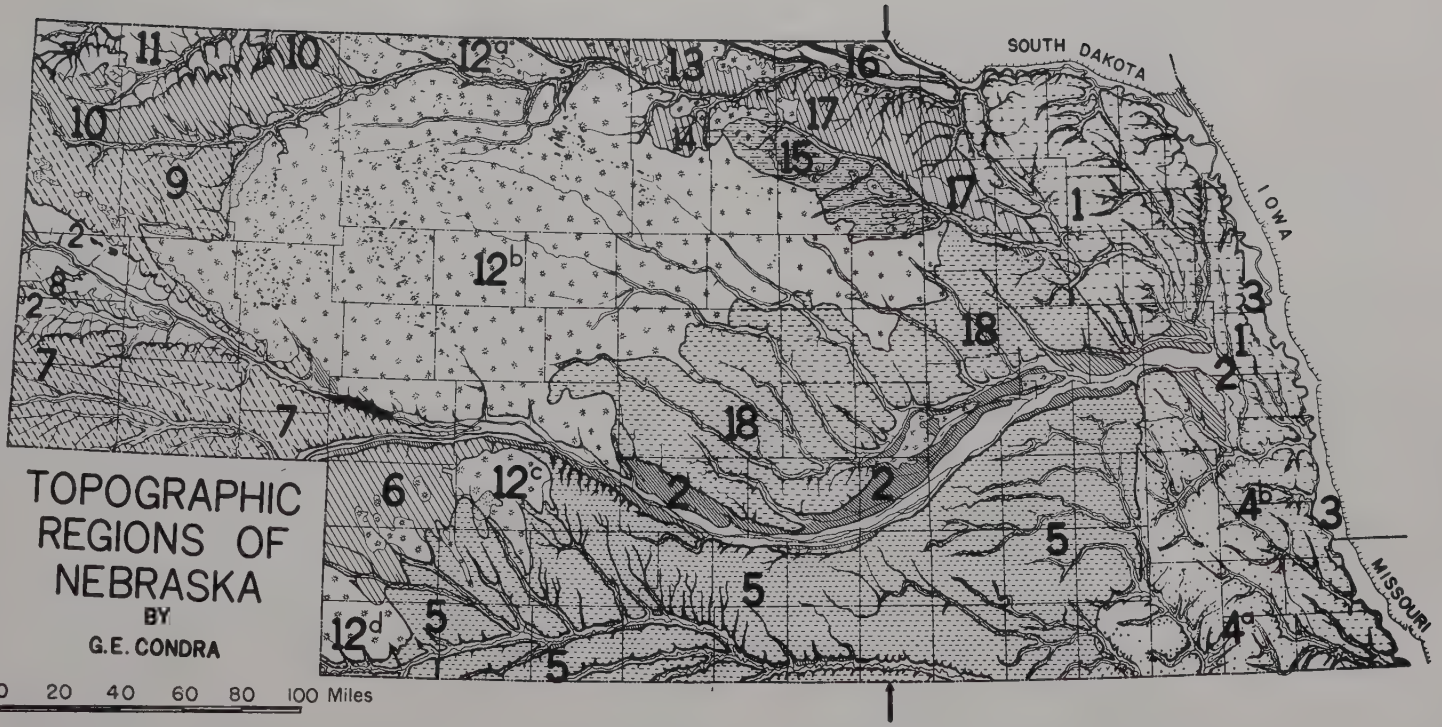

FIG. 1. Topographic regions of Nebraska. Those mentioned in this paper are: 1, Loess Hills; 2, Platte Valley Lowland; 3, Missouri River Lowland; 4, Drift-Loess Hills; 5, Loess Plain Region; 12, Sandhills; 15, Prairie Plain; 16, Boyd Shale Plain; 17, Holt-Pierce Plain; and 18, Loess Hills and Plains. Arrows show approximate western limit of True Prairie.

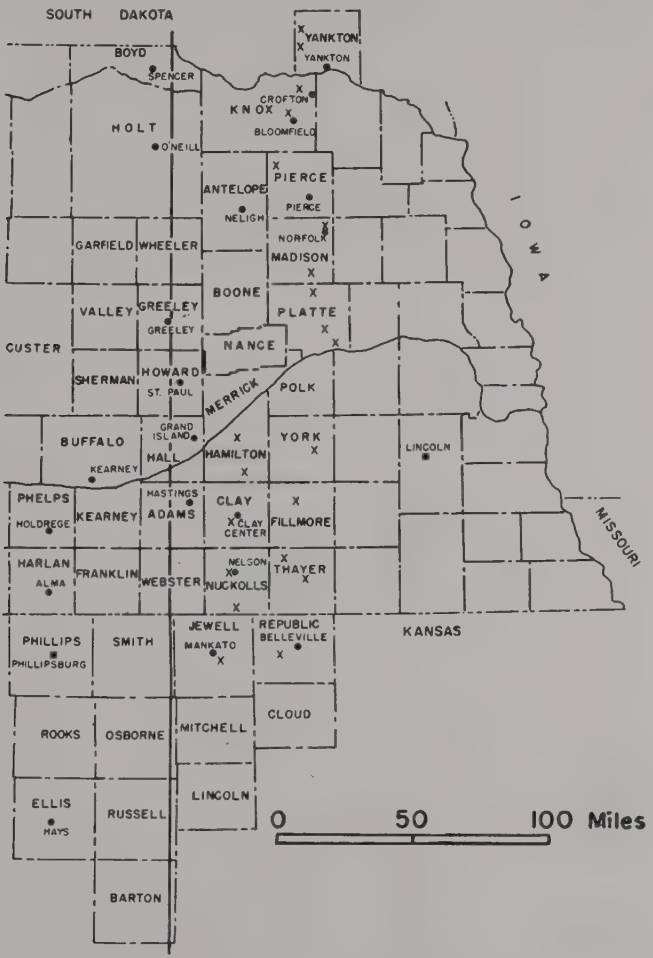

FIG. 2. Eastern Nebraska and adjacent areas with locations of counties, cities and towns mentioned in the text. Stations where extensive early studies were made are indicated by x. The heavy north-south line (98° 30′ W longitude) in the area of transition from True Prairie to Mixed Prairie represents the approximate place in which this change occurs.

to 16 inches tall at the first group of stations but 11 to 14 at the second. Similar differences occurred in 1929 and 1930 and were observed many times in following years. Big bluestem and switchgrass (*Panicum virgatum*) became much less widely distributed and showed no marked tendency toward the replacement of little bluestem as occurs eastward.

Fewer stems within the bunches of little bluestem and prairie dropseed (*Sporobolus heterolepis*) were commonly found westward. This indicated less favorable conditions for growth. In these drier grasslands, the base of the bunch was often only one-third to one-half occupied by green shoots. In well watered grassland eastward, 75 to 95 per cent of the area of the clump was normally completely filled with stems. Moreover, the small number and dwarfed appearance of flower stalks was a characteristic feature of these drier prairies except in the wettest years. The sod formed by big bluestem was much more open than were the usual dense stands elsewhere, and other vegetation was not so completely excluded by dense shade. This was also usually true of the sod of western wheatgrass (*Agropyron smithii*), hereafter designated as wheatgrass. Foliage cover on both uplands and lowlands was always reduced westward. The decrease was often 20 to

25 per cent or more compared with extreme eastern Nebraska. This was reflected in the yields of hay which became smaller as the cover became more open and the grasses more dwarfed.

Composition of the Grass Cover

On the nearly level land, little bluestem usually dominated but it was commonly intermixed with 5 to 15 per cent of big bluestem. These percentages were ascertained by extensive sampling by meter quadrats more than a quarter of a century ago. Little bluestem remained dominant over much of the terrain where ordinarily one would expect to find big bluestem. Where the land locally was slightly lower and received run-in water, the percentage of big bluestem increased accordingly until finally rather pure open stands occurred. Its turning reddish brown and often drying in summer, sometimes over considerable areas, revealed the rather unstable water supply. Many poorly drained uplands supported big bluestem where small depressions occurred. Conversely, a slight rise in the topography often resulted in nearly pure little bluestem, the bunches becoming more pronounced and more widely spaced.

Westward, blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*) gradually appeared between the bunches and later became intermingled as an understory to little bluestem. Where an additional water supply was afforded, as in depressions on hillsides or on protected north slopes and in ravines, the bluestem grasses, switchgrass and nodding wild rye (*Elymus canadensis*) formed limited areas of vegetation. In places, prairie dropseed and tall dropseed (*S. asper*) were both common to abundant, and only an occasional bunch of sand dropseed (*S. cryptandrus*) occurred. Needle grass (*Stipa spartea*), formerly much more abundant, was found rather sparingly in 1928-34. Indian grass (*Sorghastrum nutans*) occurred in 1-3 per cent abundance, switchgrass was usually not plentiful, but June grass (*Koeleria cristata*) and Scribner's and Wilcox' panic grasses (*Panicum scribnerianum* and *P. wilcoxianum*) were widely distributed. Wheatgrass, scattered sparingly through the prairie, often occupied considerable areas on compact soils, especially those with claypans, sometimes to the exclusion of nearly all other vegetation. The rapidity with which these western True Prairies degenerated into short-grass pastures under grazing was quite in contrast to the gradual change from prairie to bluegrass pastures eastward.

Changes in the area of transition occurred gradually but widely. Density of short grasses between the bunches of little bluestem and prairie dropseed greatly increased and gradually reduced the bluestem to a second rate species and nearly or entirely replaced the dropseed. Needle-and-thread (*Stipa comata*) became prominent while needle grass declined. Tall dropseed often lost its rank as a dominant, which was assumed by sand dropseed. Side-oats grama (*Bouteloua curtipendula*) took on rapidly increasing importance. June grass, though dwarfed, remained a species of considerable abundance. Wheatgrass thrived with reduced competition for light. Low-growing, drought-resistant sedges flourished in the sun as did various annual grasses.

On rolling to hilly land little bluestem mostly prevailed. Some dry knolls and steep xeric slopes were clothed with short grasses or mixtures of these with wheatgrass. Sand dropseed often became plentiful and dry slopes had patches and streaks of side-oats grama. The distinctly bunch-type of little bluestem in dry places changed to the tufted sod-mat where runoff water supplemented precipitation on mid or lower slopes. Little bluestem became intermixed with a considerable percentage of big bluestem only on the lower slopes or in ravines. Often on lowland, big bluestem was the only dominant. It also occurred in slight depressions on hilltops and hillsides, sometimes spreading to form limited areas of open sod. Vegetation of rolling land included all the grasses of level land but in amounts that varied with the topography. In these dry prairies whether level or rolling, switchgrass, nodding wild rye, and slough grass (*Spartina pectinata*) found suitable habitats quite limited.

This presents a brief glimpse of the carpet of prairie grasses as it stretched ever westward mile after mile over mostly level land into a continuously more arid climate. But with increasing drought the pattern changed as the more mesic grasses were largely replaced by species common to mixed prairie.

Change in Dominants

At stations bordering the transition zone on the west, such as Phillipsburg, Alma and Holdrege, the dominance of grasses had rather completely changed. Blue grama and buffalo grass were the most important and occurred in continuous and sometimes nearly pure stands. Elsewhere they were found as an understory to side-oats grama, wheatgrass, needle-and-thread, June grass, and sand dropseed. Little bluestem frequently remained as a principal species. Associated species were red three-awn (*Aristida longiseta*), purple three-awn (*A. purpurea*), squirreltail (*Sitanion hystrix*), and various carices—penn sedge (*Carex pennsylvanica*), involute-leaf sedge (*C. eleocharis*) and thread-leaf sedge (C. *fili-*

folia). Little barley (*Hordeum pusillum*), six-weeks fescue (*Festuca octoflora*), and false buffalo grass (*Munroa squarrosa*) were also characteristic species. Big bluestem, Indian grass, tall dropseed and other tall grasses were often found in deep, moist ravines. Thus the dominant mid grasses were of a more xeric type and the prominent understory of short grass, not found in true prairie, extended over much of the soil without the presence of a well-developed overstory of mid grasses.

Changes in Forbs

For clarity of description, forbs have thus far been omitted. They are an important part of the prairie. The increased xerophytism westward was revealed by the forbs by decrease in number of species, smaller stature, and the presence of western species. These changes became clear when one compared the forbs of the luxuriant prairies of Iowa, southeastern Nebraska, and northeastern Kansas with those in the general area of eastern Nebraska and adjacent Kansas. In the former upland areas from 65 to 90 species of forbs were usually observed in selected prairies, of about 40 to 60 acres in extent, by two men working in them for 2 to 3 hours. The lists were considerably shorter (45-60 species) in the westward area described. But in the two tiers of counties bordering the transition only 25 to 38 species were thus readily observed.

These western prairies were not especially conspicuous because of the forb population. This was due in part to the dwarfness of the plants. Often they attained no more than half the height of similar species in eastern counties of Nebraska. Many of the taller and more conspicuous ones found eastward did not occur or were much less frequent. Examples of these were *Euphorbia corollata* L., *Coreopsis palmata, Meibomia canadensis, M. illinoensis, Asclepias tuberosa, Rudbeckia hirta, Liatris pycnostachya* Michx., *Silphium perfoliatum,* and *Solidago rigidiuscula.* Many others such as *Fragaria virginiana, Gentiana puberula* Michx., and *Phlox pilosa* were not present. Conversely, western species which were rarely seen eastward occurred in and beyond the transitional area. Conspicuous among these were *Sideranthus spinulosus, Chrysopsis villosa, Gaura coccinea, Malvastrum coccineum, Allionia linearis, Solidago mollis, Astragalus plattensis* Nutt., *Callirhoe involucrata, Oxytropis lamberti, Lygodesmia juncea, Thelesperma gracile, Cirsium ochrocentrum,* and certain species of cacti. Numerous species with plants greatly reduced in size occurred throughout, for example, *Kuhnia glutinosa, Solidago glaberrima, Aster multiflorus* and *Psoralea argophylla.*

Depressed Areas

This seemingly endless carpet of grass was not uninterrupted. Scattered throughout the nearly level prairie were depressed areas which were occupied by a very different type of vegetation. These varied greatly in size. Many were small, covering only one-fourth acre; others were 80 to 160 acres in extent. The largest were sometimes 1 to 3 miles long and 2 to 4 square miles in area. The smaller depressions were only a foot or two below the general soil level but the larger ones were depressed 10 to 15 feet. Depth of accumulated water varied greatly from year to year and from spring to autumn. The shallow depressions usually became dry by mid or late summer. In larger and deeper ones, water exceeded 3 feet in depth during wet seasons. These fresh water marshes were scattered thickly over the plain. It has been ascertained that they occupied an area of more than a hundred square miles (Condra 1939). Their origin is not definitely known and may, in part, date back to a time preceding the deposition of the Peorian loess. Soils with heavy and thick claypans have developed in these depressions, *viz.* Scott and Fillmore soils. The water seeps through the heavy soil, or more probably through great cracks formed by the shrinking of the clay, hence there is no accumulation of salts. In these places, which are more or less alternately wet and dry, only adapted species of plants can exist.

One of the more abundant species and one which gave the characteristic color tone to these depressions was *Scirpus acutus* Muhl. A dark blue to green or even brownish color prevailed where dense stands occurred in places where the water was more or less continuously deep. In shallower water, perhaps only 18 inches deep in spring but nearly absent in late summer, *Eleocharis macrostachya* grew thickly in tufts 12 to 18 inches high. This perennial gave the landscape a very dark blue-green appearance throughout the growing season. In less permanently wet zones, a paludose form of *Persicaria muhlenbergii* and *Lophotocarpus calycinus* were conspicuous emersed water plants. Here also *Persicaria longistyla,* with its conspicuous masses of pink flowers, alternated with *Coreopsis tinctoria,* which gave a yellow tone to the wet land in late summer. Species of the floating stage, but persisting in very shallow water, were various pondweeds (*Potamogeton*), *Marsilea vestita, Bacopa rotundifolia* (Michx.) Wettst., *Heteranthera peduncularis* and *Alisma subcordatum. Typha angustifolia, Scirpus americanus,* and *Eleocharis acicularis,* were common. On the outer edges of the larger depressions especially, but scattered irregularly through the shallower

ones were large amounts of *Echinochloa crusgalli* and *Hordeum jubatum,* and, in places, *Phalaris arundinacea.* Other species were *Ammannia coccinea, A. auriculata, Cyperus acuminatus, Vernonia fasciculata, Lippia cuneifolia, Gratiola neglecta* Torr., and *Franseria discolor* Nutt. These plants were subjected to great variations as regards water content of soil and soil aeration.

Wheatgrass either in rather pure stands or with an understory of short grasses often bordered the deeper depressions and sometimes formed extensive hay meadows. On others, the muddy slopes became clothed with buffalo grass and blue grama. All of these grasses during dry years invaded the depressions at least temporarily. On the outer edge, the zone of grasses gave way to prairie.

Eastward Movement of Mixed Prairie During Drought

The remarkable panorama of change from one association of grassland to another was vividly portrayed on a grand scale during the terrible drought years, 1933-1941. On the westward border of the ecotone, the loss of mid and tall grasses and the gradual reduction of a typical area of Mixed Prairie to short grasses without the impact of grazing was studied during a period of seven years. The midgrasses—even the drought-resistant side-oats grama—succumbed and short grasses alone remained (Albertson and Weaver 1946). It was illustrative of a very widely spread phenomenon that occurred during that decade.

On the eastern border, the replacement of True Prairie by Mixed Prairie occurred as a result of the great drought in an area 100 to 150 miles in width in central Kansas, eastern Nebraska, and eastern South Dakota. The changes of plant populations and structure of vegetation were described in detail as they occurred in 1934 to 1941 in three widely separated native prairies (Weaver 1943). Predrought vegetation consisted mostly of the bluestems with only small amounts of wheatgrass, side-oats grama, blue grama, and buffalo grass. The chief dominant, little bluestem, mostly or entirely succumbed to drought in 1934 and 1936. Big Bluestem was greatly damaged. It finally disappeared in 1940. Wheatgrass rapidly increased each year; side-oats grama spread only temporarily. A steady increase and wide distribution of blue grama, and buffalo grass in a smaller degree, occurred throughout the drought. By simultaneous invasions of wheatgrass and short grasses, typical Mixed Prairie became clearly apparent in 1938. After seven years of drought, these grasslands were almost entirely transformed into Mixed Prairie. At this time, the entire transition region westward was also Mixed Prairie. Thus, not only in the ecotone between these two great grassland associations, but in True Prairie as well, Mixed Prairie moved far eastward along a front more than a thousand miles in length.

Partial Recovery Following Drought

With the end of the drought and replacement of deep soil moisture resulting from abnormally heavy rains—sometimes 7 to 10 inches in a single month—, a reverse movement of the prairie migration began. This has been studied yearly at several, permanent, predrought stations. The most important finding was that the recovery of True Prairie of this invaded area was remarkably slow. Wheatgrass and short grasses spread rapidly over prairie where the former occupants had succumbed to drought. But bluestems, prairie dropseed, and others species had to regain areas already occupied.

After twelve years, Mixed Prairie still prevailed over two-thirds of the land it had invaded during the seven years of drought. Wheatgrass with an understory of short grasses, mostly blue grama, or extensive areas of short grasses without an overstory, composed the bulk of the vegetation. The wheatgrass stands were rather open, since wherever blue grama occurred, it decreased the density of the wheatgrass sod, lessened height-growth, and reduced production of flower stalks. Side-oats grama was nearly always an important component of the vegetation in both of the preceding types. As in drought, hairy chess (*Bromus commutatus*) grew thickly in these drier grass types and also occurred, although less abundantly, with big bluestem. Little bluestem was infrequent, but where it did occur it was increasing its area slowly. It had largely been replaced by big bluestem which now covered approximately a third of the prairies. It was best-developed on north-facing, steep slopes and on banks of ravines, but it also occurred elsewhere, always forming a rather open sod. In places, it was intermixed with wheatgrass, and a slow invasion of blue grama was clearly apparent in places. Eastward, two or three years were required to completely shade out the bordering short grass (Weaver 1954).

Forbs had greatly recovered and were fairly abundant in some of the prairies; in others they were relatively few in both species and numbers, except certain of the more xeric types such as *Solidago glaberrima, S. mollis,* and *Kuhnia glutinosa.* But the change from Mixed to True Prairie will require a long period of time for its completion. Nature is slow but persistent. Finally, it seems clear, she will put back upon these prairies those species that were there in the first

place—long before the drought. The writers have seen this happen over a considerable area eastward (Weaver 1954).

Transitional Area After Twelve Years for Recovery

Among the many prairies examined in the four counties of the transitional area in 1953 (Fig. 2), all were distinctly of the Mixed Prairie type. On the level land, blue grama, usually with small but sometimes with fairly large amounts of buffalo grass, dominated either alone or as an understory to wheat grass. These two species always composed most of the vegetation and sometimes practically all of it. Penn sedge was extremely wide-spread and often very abundant. Patches and bunches of tall dropseed were found in most prairies and side-oats grama was an important and widely distributed mid grass. June grass was scattered more or less throughout. Wilcox' panic grass was plentiful in places; sand dropseed, plains muhly, purple lovegrass (*Eragrostis spectabilis*) and red three-awn usually occurred only in small amounts. Hairy chess, was well-represented and often it was abundant. On the level land, little bluestem was usually not present or at least only rarely, but big bluestem occurred in bunches or scattered small patches, but never abundantly.

Special mention should be made of the vegetation southward on the rough land along the breaks of the Republican River (Fig. 1). Here, there are many thousands of acres of grassland, a part of which is used for the production of hay. Upland vegetation was similar to that described. But that of the lower hillsides and canyons often benefited from favorable slope exposure. On well-protected lower and even mid slopes relatively small areas of little bluestem were found, with big bluestem occupying the ravines and the bases of slopes. But the patches and streaks of blue grama in the stand of little bluestem indicated a xeric habitat. Where the bluestem community occurred on upland, the grasses grew in sandy soil.

Erosion had produced canyons with steep banks that reached a height of 10 to 25 feet above the level bottom. These were partially protected from wind and sun and in addition they received runoff water from the surrounding upland. Amount of bluestems that occurred, especially big bluestem with a sprinkling of Indian grass, switchgrass, and nodding wild rye, varied from a wide belt, intermingled with a few shrubs, to a narrow strip of mesic vegetation including certain prairie forbs not generally distributed here. Often side-oats grama almost alone clothed the abrupt slopes or at least their upper rim. Rarely did big bluestem extend across the flat bottoms, although a ribbon-like area often demarked the course along which the water ran after heavy showers. Wheatgrass and short grasses, usually occupied the bottom, typically with an abundance of hairy chess, and often extended part way if not entirely up the slopes. Great variations in vegetation occurred with differences in the exposure of canyon walls and bottom to wind and sun. But the general vegetation in this transitional area remained Mixed Prairie.

Transitional Area in Kansas

A thorough examination of many prairies was made in Smith, Osborne, Russell, and Barton counties in Kansas, which extend southward more than halfway across the state to the Arkansas River (Fig. 2). Topography varied from nearly level to rolling, and along the breaks of streams to hilly land. Soil type (Hastings-Holdrege Series) was the same as that in Nebraska and normal precipitation was 23 to 24 inches. There was much pasture land, and mowed prairies were easily located. Practically every grass-covered area examined was distinctly of the Mixed Prairie type. In nearly all, there was a more or less continuous cover of short grasses. The dominant mid grasses were side-oats grama, wheatgrass, tall dropseed, June grass, plains muhly, and sand dropseed. Bluestems and Indian grass were often closely confined to ravines and ravine banks, but even these were sometimes clothed with tall dropseed or wheatgrass. In places, the bluestems occurred on steep north slopes, but in limited and open stands. On level land, big bluestem, especially, was found in depressions, intermixed with side-oats grama, but elsewhere its bunches were spaced well apart and usually surrounded by short grasses. Only on rocky hills, which were not plentiful, did True Prairie occur. Here impermeable rocks tend to raise the moisture supply of the intervening soil masses (Bates 1928).

The local effect of topography on vegetation was sometimes beautifully illustrated. In certain long, gently sloping ravines water supply in the shallow ditch was sufficient to support sloughgrass and a border of switchgrass with nodding wild rye. Where heavy rains occasionally caused the water to spread two or three rods laterally, bluestems and Indian grass occurred. Then abruptly, where the slope gently ascended, a carpet of short grasses and side-oats grama was spread, with bunches of bluestems scattered through it only on the lower slope. Typical Mixed Prairie covered the hillsides and hilltops.

From these and numerous earlier observations, it seems certain that the area of transition in Kansas lies due south of that thus far described in Nebraska.

Transition in the Loess Hills and Plains

The transitional area between True and Mixed Prairie vegetation continues northward in Nebraska through the central portion of the Loess Hills and Plains (Fig. 1). The general physiography of this area is that of an upland plain, ranging from almost level to steeply rolling or hilly land. Over its greater part, the plain has been thoroughly dissected and is now hilly. The hills are often 100 to 150 feet higher than the valleys between them. Comparatively level land is not extensive. Grand Island and St. Paul are located along the line of transition. Sandy areas occur where the Platte Valley Lowland extends northeastward (Fig. 1). These somewhat obscure any change in grassland communities. But soon loess hills prevail which, like those westward, are clothed with excellent short grass on the tops and upper slopes, and short grass with an overstory of mid grass on the mid and lower slopes. Typical postclimax prairie vegetation is confined to the ravines where run-in water supplements the rather low annual precipitation of 23 inches. About 48 per cent or a total of 2,250 square miles of the upland loess soils of the four major counties in the central portion of the region is covered with the native prairie sod.

The vegetation of this mixed prairie area was first described in 1948 by Weaver and Bruner but soil surveyors in 1926 emphasized "the dense growth of grama and buffalo grass," red threeawn, wheatgrass, and bluestems. The several communities or types of Mixed Prairie were delimited and described and the dominant and subdominant species ascertained. Hopkins (1951) studied the extent, composition, and environment of each prairie type. "The short-grass and mixed-grass types were of approximately equal extent in the entire area; each covered an average of about 33 per cent of all the prairie areas." He ascertained that blue grama composed 91% of the vegetation in the more xeric community and buffalo grass only about 5%. Chief components of the mixed-grass community were blue grama 50%, side-oats grama 18%, big bluestem 8% (largely replacing the little bluestem lost in the drought), species of sedges 7%, and wheatgrass 4%. Species of western grasses and forbs were common throughout. In general, these were the same as those found on the Mixed Prairie already described for the Loess Plain Region. The postclimax associes of mid and tall grasses was found on steep sides of ravines and in moist lowland. Big bluestem, especially, sometimes grew in bunches or in open stands on well-protected north and northeast hillsides. Composition of the vegetation (Hopkins 1951) was big bluestem (56%), side-oats grama (13%), various sedges (11%) and western wheatgrass (2%). Total area occupied by this type was approximately 27%. The manner in which the mid and tall grasses were replaced by short grasses, as a result of grazing, has been shown by Branson and Weaver (1953). Travelling north from the central loess hills one passes through the sandhills and enters the Prairie Plain.

Prairie Plain

The land is nearly level except for the occasional occurrence of sand hills. The ground water lies near the soil surface over most of the area. The subirrigated meadows of the broad valleys are a western extension of lowland True Prairie. The hydric vegetation varies from that of ponds and small lakes, which are abundant, through wet meadow, to the big bluestem type of grassland. Keim *et. al.* (1932) have shown that the structure of this vegetation is closely correlated with the depth to the water table. Over much of the Prairie Plain, the wet meadow type prevails. There is little if any difference in the lowland vegetation here and in the valley of the Elkhorn River at Neligh and Norfolk, in the True Prairie eastward. Moreover, the same wet prairie type extends far northwestward into the Mixed Prairie climate. From the Sand Hills, soil water for subirrigation supplements the precipitation. Consequently, the vegetation throughout its extent reveals practically no change in climate. But there is a marked change in vegetation after one crosses the Elkhorn Valley and enters the Holt-Pierce Plain.

Holt-Pierce Plain

The area of transition across this plain is characterized mostly by level or rolling land. But there are also some sandhills, and breaks occur along the Niobrara River and its tributaries. Areas of deep sandy soil characterized by sand reed (*Calamovilfa longifolia*) are extensive but infrequent. On the less sandy land covered by 18 to 30 inches of fertile black soil, which is most characteristic of the region, the vegetation revealed its Mixed Prairie nature. Where the soils were intermixed with sand, the higher and drier areas were clothed with Mixed Prairie vegetation and the wetter lowland with an open type of True Prairie postclimax. The following examples are illustrative.

A prairie near O'Neill, on level land with two feet of black soil overlying sand, consisted of about 85 per cent blue grama and 5 per cent buffalo grass. There was no continuous overstory. Scattered small patches of sand reed and bunches of big bluestem occurred. Little bluestem was rare but side-oats grama, sand dropseed, red three-awn, and a half dozen other plains and prairie grasses were present. Forbs more abundant eastward, such as *Artemisia gnaphalodes, Solidago glaberrima,* and *Psoralea argophylla,* mingled with more western ones, *Allionia linearis, Chrysopsis villosa, Opuntia fragilis* (Nutt.) Haw. *Neomamillaria vivipara* (Nutt.) Britton and Rose, *Hedeoma hispida,* and abundant *Plantago purshii.*

Conversely, on vast stretches of sand plains, needle grass or needle-and-thread either alone or intermixed, constituted 80 to 95 per cent of the vegetation. Where blue grama formed an understory on more compacted soil, these grasses were thinned, sometimes to a very light stand. Little bluestem, sandhill bluestem, sand reed, June grass, purple three-awn, but only a very small amount of big bluestem were accompanying species. A sand flora of non-grasses was intermixed with many species of True Prairie in these transitional grasslands.

On intermediate soil types, slope exposure and run-in water caused great variations in distribution of vegetation. But even where postclimax, lowland prairie occurred, the stand of bluestems was far less dense and other vegetation much more open than in prairies eastward on this plain or at Pierce, Bloomfield, and Crofton (Fig. 2.). An extensive examination revealed clearly that the region of transition from True to Mixed Prairie passes through the central portion of the Holt-Pierce Plain. Upon crossing the Niobrara River, one enters the Boyd Shale Plain.

Boyd Shale Plain

Prairies selected for study were all located on the level or sloping land characteristic of the general topography. Here the normal precipitation as at O'Neill, is about 22 inches. The steep bluffs of the deeply channeled Niobrara and of the Ponca River afforded many sheltered and well-watered habitats which resulted in a westward extension of True Prairie grassland. On typical, nearly level areas of "hard land," blue grama with some buffalo grass formed an almost continuous layer of vegetation. The upper story consisted of wheatgrass, side-oats grama, and sand dropseed, all abundant. Only infrequently were the bluestems found and then always in slight depressions. Extending outward a short distance from broad shallow ravines with run-in water, open stands of big and little bluestem intermixed with side-oats grama, various sedges and Kentucky bluegrass, occurred. There was often an understory of short grasses. The clayey nature of the soil was indicated by the presence of slough grass in the wettest places, a species rarely found in the loess hills.

In other prairies on rolling land, strips of True Prairie grasses and forbs bordered the lower parts of the more protected slopes. Extending from the ribbon of slough grass in the wet ravine bottoms to the top of the ravine banks, they usually gave way, often abruptly, to mixed prairie. Here the short grasses were overtopped by wheatgrass and side-oats grama or they occurred between the bunches of little and big bluestem scattered sparingly over the hillsides. On crests of hills and those with broad level tops, the bluestems and more mesic forbs were absent. Here the short grasses prevailed or short grass with wheatgrass and side-oats grama. Representative forbs from both true and mixed prairie were found. They were most abundant and the societies more pronounced on the less xeric sites. Chief societies were *Amorpha canescens, Artemisia gnaphalodes, Psoralea argophylla, Echinacea pallida, Solidago mollis, Sideranthus spinulosus, Ratibida columnaris,* and *Artemisia frigida.*

Another type of vegetation common on many hard lands was that of blue grama under a thick overstory of needle-and-thread. Side-oats grama was usually common. Other grasses lightly intermixed were needle grass, June grass, penn sedge and other sedges, red three-awn, and plains muhly. Little bluestem was not common but bunches and patches of open sod of big bluestem grew in slight depressions or where run-in water supplemented the supply furnished by an approximate 22 inches of precipitation. This type of Mixed Prairie prevailed over the hills and uplands; only in the deeper ravines was it replaced by True Prairie. In other prairies, belts and patches of True Prairie vegetation with its characteristic plant societies, alternated with even larger fragments of Mixed Prairie with its similarly distinctive forbs of the plains.

From these data one must conclude that a transitional area where True Prairie vegetation gives way to that of the drier Mixed Prairie occurs in the eastern part of the Boyd Shale Plain (Fig. 2).

Summary

The very gradual changes in vegetation from True to Mixed Prairie have been described. These occur over a broad ecotone about 50 miles in width as shown in Figures 1 and 2. If the

place were to be indicated by a single line, one (98° 30′ W longitude) extending along the eastern side of Barton County to Smith County in Kansas, and through Hastings, Grand Island, and Greely to O'Neill and Spencer in Nebraska (Fig. 2) would be representative.

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SOME LOWER MISSISSIPPI VALLEY FLOOD PLAIN BIOTIC COMMUNITIES; THEIR AGE AND ELEVATION

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Introduction

Forest development on the flood plain of a large river is important in many ways. The constant shifting of islands, bars, and channels, illustrated in Fig. 1 provides new ground for beginnings of seres, many of which stop short of the climatic climax so long as flooding continues. This makes the large river flood plain exceptionally useful, and perhaps as important as sand areas in the study of ecological principles.

Those who live adjacent to great rivers are impressed with the great forces involved. Floods drive residents to high ground, often destroy utilities which they have set up with great labor, or crops that they have planted. Tiptonville, Tennessee, lies to the west of the south end of Reelfoot Lake. In about the year 1880, the river occupied the channel shown in Fig. 2 adjacent to the northwest corner of the village. By 1885, the river was taking away land, houses, and business establishments. By 1900 half of the inhabitants had moved southeastward and built new homes. It appeared that the entire village might be washed away and Reelfoot Lake drained a little later. However, the river began shifting westward and

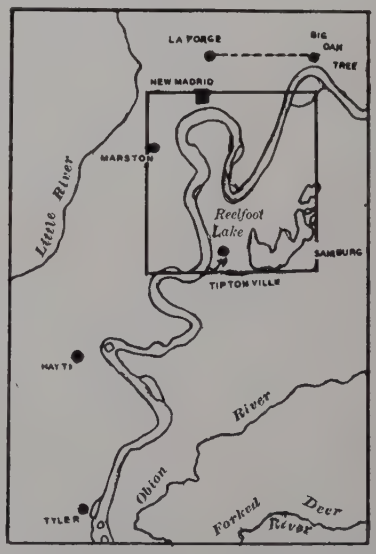


Fig. 1. The area of general observation (approximately 40 miles from north to south. The smaller rectangle is the area of special study covered in Figs. 4a and b.

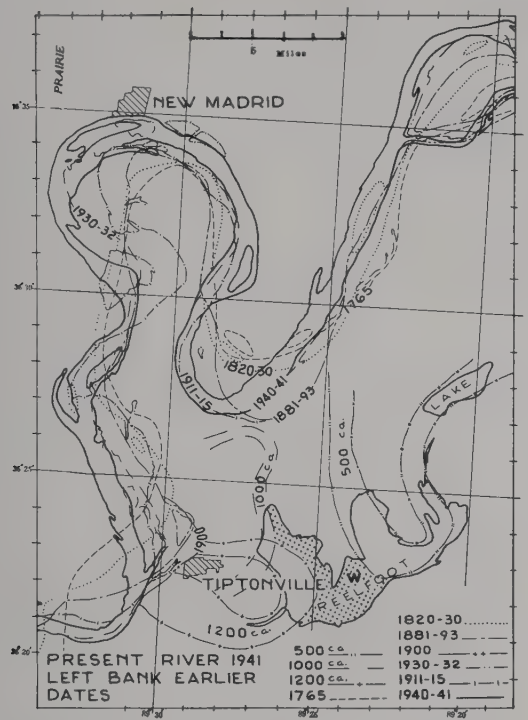


FIG. 2. Showing the courses of the channel of the Mississippi River 500 to 1941 A.D. Approximate dates from Fisk (1944). The dotted area was probably flood-plain forest at the time of the earthquake. The prairie west of New Madrid is unknown as to character. The words Lewis Prairie appear on some maps at the point indicated. The W near the lower right hand corner is the area from which furniture walnut was removed in the 1880's (information by R. C. Donaldson).

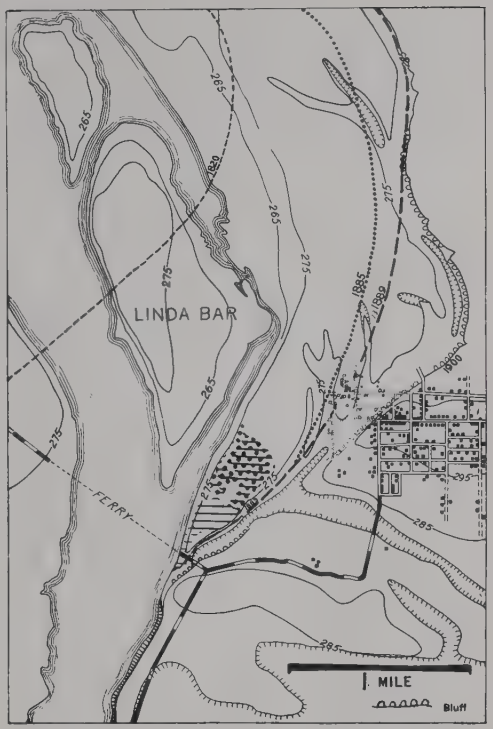


FIG. 3. The encroachment of the river onto the village of Tiptonville, 1885 through 1900. (After Donaldson 1942.) The legend of Fig. 4a has been added to the area near the Tiptonville Ferry which shows the condition in 1932. About one-fourth of the area covered with the legend has been swept away by the river since the mapping was done. The legend of cottonwood and of hackberry-gum has been combined to fit the conditions.

built up two islands. Deposits have since raised the area which was river bottom at the time the village was threatened, to the 285 ft. level, 35 ft. above mean low water. It now is being cultivated. The principal object of this is to suggest a time schedule for the development of the principal flood plain communities.

Flood Plain Habitats and Areas Studied

There are two types of flood plain habitats: (a) terrestrial, which are dry at low water, and (b) aquatic, which are covered with water the year round or nearly so. They are discussed in the last section of the paper.

Two sub-types of terrestrial habitats can be distinguished: (a) one group which lies close to the river channel, characterized by short annual submergence and molded by the gradual shifting of the river from one side to the other in the area known as the meander belt, and (b) a second or long submergence type occurs on low ground where flood water stands for very much longer periods than in the meander belt. This is due to various causes such as subsidence, slow aggradation in the valleys of the last glacial period, or convergence of drainage systems resulting in very large amounts of water, as in the lower St. Francis and White River areas of eastern Arkansas.

The principal area of study centers near Island No. 10 of the Mississippi River. Its eastern boundary is the loess bluffs which rise 150 to 180 feet. The southern boundary is the southern tip of Reelfoot Lake. The northern boundary is at New Madrid, and the western boundary near Marston, Missouri. With the exception of the extreme western portions, the area lies in the meander belt. As to the western portions just west of the river, between the latitude of New Madrid and that of Tiptonville, there is a relatively high ridge which could have resulted from overflow of the Mississippi into Little River of the St. Francis drainage. This ridge is a part of the meander belt. Farther

to the west is a vast, nearly level plain extending west for 50 miles to the St. Francis River and Crowley's Ridge. In time of flood before the days of levees, one could cross this entire area in a row boat. In some parts of the Little River drainage, water stands for much longer periods than in the meander belt and the habitat is of the long submerged type.

The semi-natural biotic community relics of the area of special study (Fig. 1) have been investigated by graduate students accompanied by the writer in March or April for 21 years beginning in 1929. These studies provided many records[1] of both plants and animals. In 1943, it was decided to do some serious work on some of the terrestrial communities. Summer and autumn work was added. Fisk's (1944) paper gave impetus to the studies. Since 1929 the last remaining nearly virgin timber at cultivatable levels outside the Reelfoot Lake Park has been removed. The state cut the last virgin stand of cypress-ash in 1950 because it was mature and would grow up again. Also at the White River area, the timber was in the process of being removed from Big Island in 1943.

The Reelfoot Lake Park and Fish and Game Preserve has been important in the researches. It was established by the Tennessee Legislature in 1925. At that time the state obtained full title to the Lake from real estate operators after many years of litigation. An overflow spillway was provided and post-earthquake drainage into the Obion River facilitated. Only a narrow strip of land outside the lake was acquired by the state except on the west side. Here a large tract was enclosed by about six miles of deer fence and deer introduced in the mid-1930's (see Fig. 5). In the inhabited areas around the south end of the lake, the strip of state land is rapidly being taken over by private interests.

Two portions of the reservation have been made a National Waterfowl Refuge. The aquatic and marsh vegetation is subject to modification to increase duck foods.

A secondary area of study is Big Island in the White River near St. Charles, Ark., 125 miles south of Tiptonville at 34° 20′ N. The White River National Wild Life Refuge is located there. The island is sometimes under 30 ft. of water for several weeks. It had been under more than 10 ft. of water for more than a month in July, 1943, when a short study was made there.

The Short Submergence Terrestrial Habitats and Communities—the Meander Belt

The short submergence habitats at 25 ft. and more above mean low water are generally cultivated after the communities are removed. The long submergence habitats are not ordinarily cultivated.

In arriving at the conclusions present in the discussion, (a) the age of the deposits on which the trees are growing and (b) the height of the deposits above mean low water have been given serious consideration (Table I). The dating on Fisk's (1944) Fig. 33 and all available maps of Mississippi River Commission and the U. S. Engineers were utilized.

The areas of general observation and of special study are included in Fig. 1. A region including western Tennessee, eastern Missouri and Arkansas was shaken by a teriffic earthquake in the winter of 1811-12. It began with the first severe shock Dec. 11, 1811. Some land was uplifted, but the oxbow ponds, cypress sloughs, and flood plain forest on the site of the present Reelfoot Lake sank 25 ft. at the south end of the present lake and 5-10 ft. near the center, and well toward the north end, thus creating the present lake.

Table I. *The mean low water of the Mississippi River in 1937, and the heights which are just above flood water in the adjacent areas. From the 1937 Mississippi River Levee and River Charts, U. S. Engineers Office, Memphis, Tenn. Figures are in feet above mean Gulf level.*

	Mean low water 1937	Levels just above flood waters	Cultivation
North of Hickman	270.0	315	295
Hickman	268.8	314	295
Island No. 8	266.6	312	292
Ky.-Tenn. Line	265.2	310	290
Old Slough Landing	263.3	308	283s*
New Madrid	260.7	306	285
Darnell Pt.	253.0	298	278–280
Tiptonville Ferry	249.5	295	275
Merriwether Bend	248.3	293	270
Hayti	244	289	260
Cottonwood	240	285	255

*Sunkenlands.

[1] The use of metric and English systems of measurement follows the usage in research papers in the fields concerned. Names of trees both common and scientific, follow Little (1953) with regional modifications noted. Other plant names follow Fernald (1950) except that "var." is not used for varieties. Common names of birds follow the A.O.U. Checklist. Names of mammals follow Anthony (1928); of snakes, Schmidt and Davis (1941). Names of lizards follow Smith (1946); of salamanders, Bishop (1943); of frogs and toads, Wright and Wright (1949); of spiders, Comstock (1948). The names of beetles follow Leng (1920, 1939); of Diptera, Curran's North American Diptera (general only). Leaf hopper nomenclature follows DeLong and Knull (1945) checklist. Names of the bugs (Heteroptera) follow Blatchley's Heteroptera (1926). Author's names appear in the case of species not in the lists cited or which bear names in dispute.

In the area of special study (Fig. 1), the original biotic communities have been unusually thoroughly obliterated from at least 98% of the cultivable land. The remaining 2% is second-growth forest in and about Reelfoot Lake Park. Also there are perhaps a score of pre-earthquake trees about farm buildings. The known relations of these to climax and sere has had an important bearing on the conclusions drawn regarding the late forest stages. The primeval communities within the area west of the Mississippi are even more thoroughly destroyed than near Tiptonville.

The forested land too wet to cultivate is (1952) in second-growth forest as a result of being thinned in the cottonwood areas and repeatedly selectively thinned on the older flood plain about Reelfoot Lake. The small area of upland forest included in Fig. 4b is not considered. In the area of general observation outside the area of special study, the same general statements apply and it need only be noted that obliteration of original communities has been less complete east and northeast of New Madrid than elsewhere. The areas about the Obion and Forked Deer Rivers in the southeastern one-fourth of the area have not been investigated at all. The large influent animals of the region have been extirpated or their populations reduced to biotic impotency for at least a century.

Figs. 4a and 4b represent an attempted reconstruction of the plant constituents of the biotic communities of the area of special study. They are represented as they probably would have been if there had been no interference on the continent by European man.

1. Flooding

Nearly every year, two or more early stages of flood plain forest are inundated. The length of time varies from a week to two and one-half months. Usually the flooding comes early in spring, but sometimes as late as May or June. Usually there is more than one period of submergence.

Only a little attention has been given to the kind of material in the deposits. While the river in the stretch from New Madrid to Tiptonville Ferry was moving mainly westward, our cottonwood study area near the Tiptonville Ferry received a layer of fine silt each year. Unfortunately, these layers were not measured but each amounted to several inches as a minimum. During to western movement, the height of the flood and the period of submergence determined the size of particles and amount of fine silt. On the other hand, in 1949 the river began moving eastward in the Darnell Point area N. E. of III Fig. 4a and started cutting away a considerable area of cottonwood forest. The current through the Donaldson cottonwood area at X was swift and two or more feet of sand were deposited. Unfortunately the forest had been thinned by a 1947 cutting, but seedlings of six or more species of trees were numerous in 1952, probably favored by both the sand and the thinning. If the river does not sweep away all of this cottonwood area but shifts again to the west while some of it remains, the sand will be covered with silt. Alternating layers or deposits of different sizes are to be expected in the meander belt.

2. Sand-bar willow (Salix interior) associes

This willow grows in masses from seed and forms thickets through stolons. Army Engineers maps show willows down to 5 or 6 ft. above mean low water. They also must have a portion of the crown out of water during part of the summer of their second year, in order to survive. In their second and third years, the sand-bar willows tend to cause more sand to be deposited and to hold that already in place. The full grown sand-bar willow is a small tree which produces roots along the entire length of its trunk when buried in sand. It is attacked by a large array of insects and is occasionally used as food by deer.

Mr. J. A. Putnam of the U. S. Forest Service in a personal communication (1952) stated that it is very doubtful whether sand-bar willow has any necessary or essential relation to the establishment of black willow or cottonwood. "Black willow and/or cottonwood soon take over new bars and points, whether preceded by sand-bar willow or not. The principal requisite seems to be concurrence of an appropriate river stage with seed present. If they get nearly an even start, the black willow and cottonwood outgrow and smother the sand-bar willow while it is still in the sapling and very small pole stage. If a full stocking of sand-bar willow attains a few feet in height in advance of seeding of the other species, due to their intolerance they cannot establish themselves and simply have to wait for the breaking up of the stand. This breakup is always accomplished in a relatively short interval by the inherent very early maturity of the species if not by further very heavy deposition."

3. Black willow-cottonwood (Salix nigra-Populus deltoides) associes

Cottonwood seedlings appear in thick stands on well-drained ground and willows in low moist spots at levels from 15 to 30 feet above mean low water. The seeds of both willow and cottonwood are dispersed in spring, the willow a little earlier than the cottonwood. They germinate

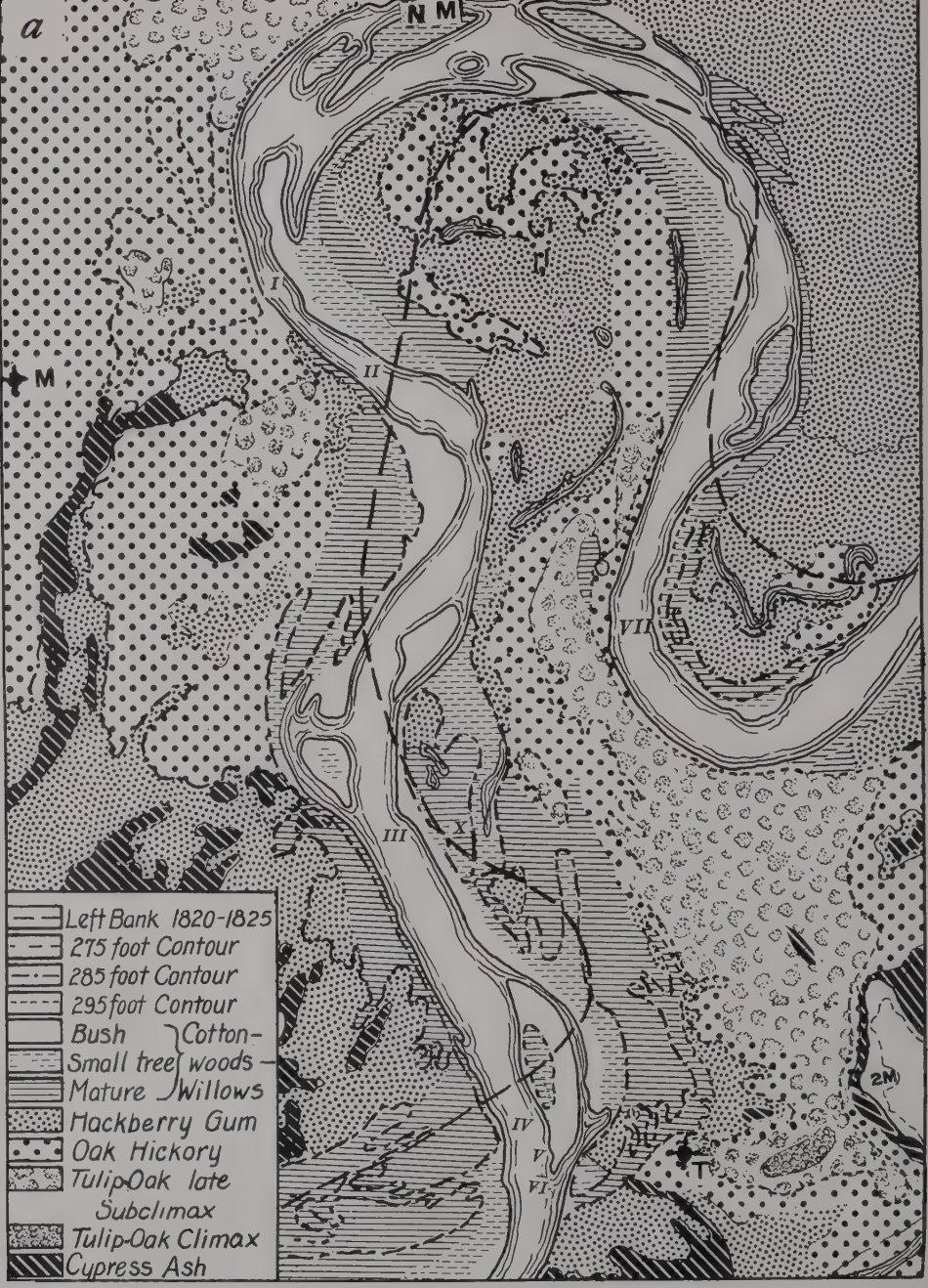
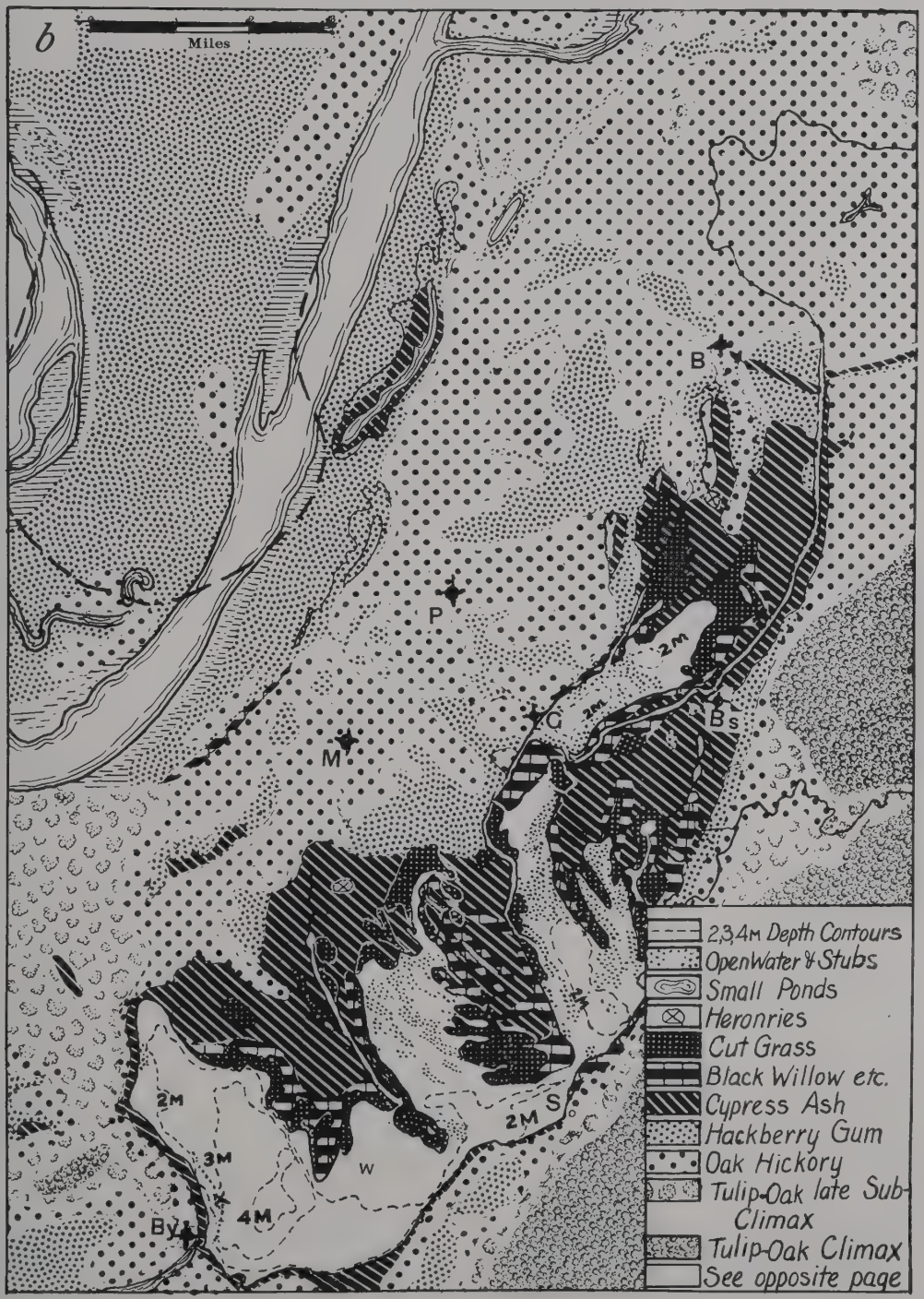


FIG. 4 a and b. The reconstructed vegetation of the Reelfoot Lake-Marston, Mo. area. *a*. The small circles with crosses and capital letters locate villages as follows: N. M., New Madrid, Mo.; M., Marston, Mo., T., Tiptonville, Tenn. The Donaldson area of virgin cottonwood is marked by X to the right of III (Darnell Point) in the river. The existing tulip-oak is to the right and a little above the X. Some contour lines are partially shown. I-VI in the river channel are to locate features on the mainland directly to the right, or left. VII is to the left of the center of Island Number 10. Just above the VII at the left, a circular pond is indicated but exaggerated in size. It was produced by the breaking of the levee in 1937. It probably started by water whirling around farm buildings. Its depth was 80 ft. immediately after the flood. *b*. The small circles with crosses indicate villages B., Bondurant, Ky.; P., Phillippy, Tenn.; By, Boyette's Landing; S., Samburg. The tulip-oak climax shown is on the upland. The dots marked "stubs" are living cypress trees sunk at the time of the earthquake. Curved line of dots in front of By is the line of cypress stubs suggesting the A.D. 1200 channel. W locates source of walnut. On the land surface, the 5 ft. contour lines are omitted entirely as they are a poor guide on such a flat surface.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Black Willow etc.
Cypress Ash
Hackberry Gum
Oak Hickory
Tulip-Oak late Sub-Climax
Tulip-Oak Climax
See opposite page

very quickly and are of notable size by midsummer. They cannot be profitably removed from agricultural lands if allowed to grow during the second season. In such stands self-thinning is rapid and extensive.

a. Shrub-sized cottonwood-willow with bare silt areas.—In early spring when not inundated, willows and cottonwoods 5 or 6 ft. high are usually accompanied by red earthworms and some dipterous larvae. Often slugs are present on the soil surface. By late summer (after the waters have receded) cocklebur, grasses and other pioneer herbs grow upon the bare areas. This is especially true where the substratum is silt. These plants by the beginning of September are occupied by a large series of native insects, usually common ones, well-known in cultivated fields. Such an area which was under water during most of April, 1943, on September 7, supported 38 individual insects, spiders, etc., per m^2 . These belonged to 19 different species. There were unidentified leaf hoppers, lepidopterous larvae, cucumber beetles (*Diabrotica 12-punctata*), tarnished plant bugs (*Lygus oblineatus* (Say)), cocklebur mirids (*Ilnacora stalii*), stilt bugs (*Jalysus wickhami*, and tree crickets (*Oecanthus nigricornis* Wlk.) all of which feed upon the plants found in the area and also on so-called weeds of cultivated fields. There were 13 specimens of the cocklebur fly (*Euaresta aequalis* Loew.) which feeds on cocklebur seeds. Specimens of the ant (*Pheidole vinelandica* Forel) which is a seed-storing ant were found. These were accompanied by a series of predators including the red lady beetle (*Coleomegilla maculata*), the predatory mirid (*Deraeocoris peocilus* (McI.)), four species of spiders including a crab spider (*Misumenops celer* Hentz), a long bodied spider (*Tetragnatha elongata*, the spiny abdomen spider (*Acanthepeira stellata* (Walck.)), and a young crab spider (*Philodromus*). It appears from the submergence that some of these insects and other animals would have necessarily moved into the area from higher ground. The young of the spiders may have been in the adjacent taller willows. It is altogether possible that the larvae of the cocklebur fly withstood the submergence in the seeds on which they were feeding.

b. Small tree-sized willows and cottonwoods (Fig. 3; VI of Fig. 4a).—The area of special study was about 20 feet above mean low water in 1937 and had been built up considerably by silt deposition in the 10 years following. Cottonwoods and willows often grow together, the latter on the lower ground. By the time they reach small tree size, silt deposition may make them appear on the same level. Small-sized individuals of the trumpet vine (*Campsis radicans*) occur in some numbers, and occasionally there is a sycamore seedling and young grape vines. At our small tree study station, the stand was 90% cottonwood and 10% willow. In early spring, there were earthworms in the soil along with a considerable number of Collembola and a few ground spiders on the surface. There were usually a few scarabaeid larvae, dipterous larvae, red mites, staphylinids, and spiders. The surface of the ground showed swamp rabbit pellets and occasional slugs. The willows and cottonwoods supported only a small number of insects such as leaf hopers, etc., in early spring. The herbaceous vegetation was often entirely wanting. About twenty species of birds occurred quite commonly in this area and in the earlier and next later stages (see following section).

By late summer because of the thick stand of trees and rather dense shade, there were only scattered herbaceous plants, usually the same species as those growing in the open. Those growing in the shade supported only a few animals. However, the woody plants showed a rather large group of insects and spiders amounting on, September 7, 1943, to 35 individuals on an estimated m^2. This included tree cricket nymphs, a considerable number of willow sawfly larvae, a few lepidopterous larvae, a few leafhoppers and 8 spiders, 7 of which belonged to different species. Those old enough to be identified were *Theridion frondeum* and *Tetragnatha limnicharis* Seeley; these doubtlessly feed upon the leafhoppers, cricket nymphs, etc. The spiny soldier bug (*Podisus maculaventris*) which feeds upon other insects, was present and is capable of dispatching sawfly and lepidopterous larvae. This area was under only slightly less water in the spring of 1943 than the area of young willows.

c. Mature cottonwood-willow associes (IV of Fig. 4a).—Two areas near Tiptonville were used; one near the ferry southwest of town and the other, Mr. Donaldson's virgin area was five miles northwest of the village. The submergence of both these areas was for a shorter time than the earlier stages. Both were 25 to 28 feet above low water. They were studied several times in spring and in the summers of 1943, 1947, 1948, and 1952. The trees were more than 18 inches in diameter. The trumpet vine comes in with the cottonwood and willow on the ridges and persists up to the hackberry stages. Poison ivy (*Rhus radicans*) is frequently more abundant on the willows of the flats than elsewhere. Here it appears in the succession before the grape (*Vitis* sp.) which is abundant on the ridges. In some areas pepper-vine (*Ampelopsis arborea*) takes the place of the

trumpet vine and the latter is almost absent. The trumpet vine, poison ivy, grape, pepper-vine, blue-vine (*Ampelamus albidus*), sometimes buckwheat vine (*Brunnichia cirrhosa*), and morning glory (*Ipomoea lacunosa*), together with other annuals, make a mass of vines covering tree trunks and binding and tangling them together so as to make passage very difficult except on old trails. In some open spaces where there has been disturbance they cover the ground in a hip-deep tangle. The density and luxuriance of the vines varies from year to year. This growth tends to retard flood waters in spring and thus increase deposition of silt.

Our ferry area of study showed approximately 60% cottonwood and 40% willow, counting the full-grown trees of 16 inches (40 cm.) in diameter and larger. There were a few sycamores, usually less than one per cent of the total large trees. The principal shrub was elderberry (*Sambucus canadensis*). There were also occasional rough-leaved dogwoods (*Cornus drummondi*).

In the spring when these areas were not under water, ground collections of animals were large. This means that the animals must survive flooding quite well. Slugs, red annelids, ground beetles, millipeds (*Pseudopolydesmus serratus* (Say)), adult insects, fly larvae, and bettle larvae, were numerous. Snails (*Succinea*) and occasionally centipedes occurred. Collembola increased in comparison to the preceding stage. Fallen logs with loose bark had a rich fauna also. Pyrochroid beetle larvae and carpenter ants occurred in considerable numbers. Centipedes and millipeds were numerous and both white and red earthworms occurred. The snails (*Zonitoides*) and slugs (*Derocera*) occurred in considerable numbers. The low vegetation was inhabited in mid-April by crane-flies, syrphus flies, green midges, muscoid flies, and mosquitoes, all of which were numerous. Leafhoppers, snout beetles, and minute spiders were numerous in the trees.

The following birds which were common to the first three cottonwood substages of the relatively small area involved (40 hectares; 100 acres), had been listed together each mid-March or early April over a number of years. Those most constantly present are shown with the numbers recorded by S. C. Kendeigh in 1947. The ones which are starred are primarily insect eaters and thus feed on those insects listed above: * Carolina wren (20), * white-throated sparrow # (16), * blue-gray gnatcatcher (14), *towhee (14), cardinal (13), * myrtle warbler # (12), * Carolina chickadee (9), crow (9), downy woodpecker (3), tufted titmouse (3), brown thrasher (3), song sparrow (2), flicker (2), hairy woodpecker (2), barred owl (2), robin (2), red-bellied woodpecker (1), yellow-bellied sapsucker (1), brown creeper (1), catbird (1), and red-eyed vireo (1). Some individuals of several species in the above list nest in the area (those marked with # excepted) but no actual data have been secured.

The mid-summer vine tangles have been described. The herb layer is usually poorly developed. There were, however, a few cockleburs and ironweeds (*Vernonia*) in spaces not covered with vines or the thorny bramble (*Rubus*).

Late summer collections were made from the lower vegetation in 1943 which gave an estimate of 125 insects and spiders per m^2. This was following an April flooding. In 1947, following a June flooding, collections from the similar Donaldson area yielded about one-third as many individuals. This suggests that June flooding and summer drought probably reduced both number of species and individuals.

The four most abundant groups of 1943 appeared in the two years in numbers indicated by the first parenthesis and in 1947 as indicated by the second parenthesis:—unidentified leafhoppers (71) (9); Red striped leafhopper (*Graphocephala verusta* (4) (5); Green leafhopper (*Empoasca* sp.) (12) (1); plant bug (*Phytocaris tibialis*) (8) (0).

The following identified species occurred in 1943 and not in 1947: stink bug (*Podisus maculiventris*); stilt bug (*Emesaya brevipennis*). Beetles were not numerous except for the triangular beetle (*Anoplitis inaequalis*). The parasitic hymenopterans were represented by *Cryptus fraterculus* (Prov.) and *Microgaster epagoges* Gah. The dipterans were poorly represented by *Plastoneurus vagans Leow.* and the spiders and phalangids by the nursery web weaving spiders (*Pisaurina mira*) and the harvestman (*Leiobunum vittatum* (Say)).

As compared with earlier stages, the mammals of this area increased. The opossum and raccoon were common and the white-footed mouse had increased. Gray squirrels were present and were seen occasionally.

In 1947, a virgin stand of commercially mature cottonwoods was selectively harvested for lumber from the Donaldson area north of Tiptonville (X of Fig. 4a). In 1912, this area was in the center of the river channel. In 1937, it was about 28 feet above mean low water. Subsequent flooding, notably in 1952, has probably raised it to 30 ft.

The cottonwoods were 20-24 inches in diameter at breast height and showed 20± rings in 1947. Willows of similar size on the lower ground, or in some areas mixed with the cottonwoods were also heavily vine-covered.

Up to about 18 years of age, the cottonwoods and willows are of approximately equal vigor and growth rate. Beginning about this time, the willow declines in vigor while the cottonwood continues to grow and remains in vigorous condition for 10 to 20 years longer. Williamson (1913) gives similar but longer periods for areas farther north. In the Reelfoot Lake area, the cottonwoods grow in diameter at the rate of 0.85 in. per year while the average of five of Williamson's data for Iowa is 0.41 in. per year.

In both 1951 and 1952, the Donaldson area was submerged throughout the late winter and spring. In 1952, much sand was irregularly deposited. One old channel was filled with sand but still barren. Other depressions of considerable size were filled and one water hole excavated below a fallen tree. Seedlings of cottonwood were mainly from 1952 germinations. The depressions and other scars constitute openings in which cottonwoods survive to grow after the principal stand is commercially mature. The resulting trees complicate the later forest stages.

d. The old cottonwood-willow community.— The difference in length of period of vigor and growth of the two dominants is one basis for changes after 20 or more years in an equal-aged stand of cottonwood-willow forest. Another is the shade tolerance of trees with seeds which can germinate under the substratum condition in cottonwood-willow.

Seedlings appeared in the old cottonwood stand near the Tiptonville Ferry. They are listed as they were four years after a thinning in the order of abundance below with number of individual given followed by diameter in inches: box elder (*Acer negundo*) 40 (5″-10″); red maple (*A. rubrum*), 35 (4″-7″); sycamore (*Platanus occidentalis*), 10 (9″-13″); pecan (*Carya illinoiensis*), 6 (1″-3″); elm or American elm (*Ulmus americanus*), 3 (1″-8″); black locust (*Robinia pseudoacacia*), 2 (1″); hackberry (throughout the Mississippi alluvial plain, Putnam and Bull 1932) or sugar berry (*Celtis laevigata*), 2 (1″-3″). The study was made in 1948 but most of the seedling species had been noted in 1943 and 1944. A few sweetgum (*Liquidambar styraciflua*) had disappeared or were not found. Counted from the cottonwoods as seedlings, this area is estimated to be about 40 years old. It is an addition to an island, some of which still remains to the north of the area of study, which was a sandbar in 1896 when granted by the state to private owners. This was 51 years old in 1947 and is now nearing a hackberry-gum stage (opposite IV of Fig. 4a).

Considering all the tree species growing in the area as shown in the list above, plus the cottonwoods and willows, shade tolerance appears to be important. Applying Baker's (1949) tolerance table, it appears that cottonwood and black willow have the lowest tolerance of the group while soft maple and boxelder have the highest. This enables the latter to seed under the shade of the cottonwoods and willows as soon as the soil and litter conditions are suitable. One result is stands of soft maple and box elder overtopped by old cottonwoods, which occur occasionally.

The seedling of the post-cottonwood trees appear after the accumulation of organic debris from leaves, small plants, twigs, animal droppings and carcasses, has been operating to modify the soil for some time. Meanwhile earthworms and burrowing arthropods have worked the material over. Flooding has more often buried the accumulation than it has removed it.

It is probably correct to assume that pecan, elm, mulberry, black locust, gum, and hackberry are governed more by soil conditions than by light and shade since they are less tolerant of shade than boxelder and soft maple.

The condition of the woods from the cottonwood stage to a hackberry-gum stage which is recognized by Putnam and Bull (1932: 41) (the type trees are listed in the next section), is not well represented since there are no stands in the Reelfoot-Marston, Mo. area. However, the area in Missouri opposite the Tiptonville Ferry is an old cottonwood stand probably thinned several times. It contains in addition to cottonwood and willow, representatives of ten other species in about equal numbers. Eight trees appearing as seedlings in our old cottonwood stage were present and in addition, green ash (*Fraxinus pennsylvanica*) and dogwood (*Cornus* sp.)

The designation "hackberry-gum" has met with objection from local people and from some foresters. Putnam thinks hackberry-gum and hackberry-elm result from timber-cutting which is probably true near Reelfoot Lake. The 1912 river maps show an area which was water in 1930 marked "hackberry" and nearby "gum." Eighty-two years is a rather short period for these trees to reach prominence unless a single flood brought the substratum up to the necessary level. Cottonwood harvesting in the 1890s is not very probable.

2. Hackberry-sweetgum forest (hackberry-gum: Celtis laevigata-Liquidambar styraciflua) communities[1]

This stage appears quite definite but still subject to much variation as to composition. Four areas of hackberry-gum were available for examination, and in all, either one or the other of these trees was the principal one.

As to the communities in which gum predominates, two areas were studied. One of these was a (0.4 hectare) transect across the ridge at the south end of Reelfoot Lake near Samburg. It sloped toward the lake where there were sycamores; there was no evidence of cutting but considerable trampling. It contained 25% gum and only 4% hackberry and was representative of the south end of the lake shore where there is considerable loess in the substratum. In 1928 and for about ten years thereafter, there was an adjacent 15 hectare area of hackberry, and its associates with a little gum, most of the gum had been removed according to a reliable informer.

A second area is at Hayti, Missouri, barely 30 feet above mean low water, perhaps less. The Hayti area is on low but well-drained ground; in the Hayti North Side Park. There were 360 trees on these 4 hectares with an average diameter at breast height of approximately 30 inches. The composition in per cent was sweetgum 71 (this could have resulted from seeding on an abandoned field), hackberry 8, sycamore 17, elm 1, and pecan 1. In addition there were one or two trees each of 9 species of common trees which may tolerate annual flooding; viz.: Shumard oak, black oak, overcup oak, pin oak, honey locust, red maple, Kentucky coffee tree, bitternut hickory, and shellbark hickory, total 2%. The undergrowth had been removed.

Of the communities in which hackberry is predominant, one is located one-half mile south of Grays Landing (Fig. 5), in Reelfoot Lake Park. The area was about 3 hectares and contained 284 trees, of 6 in. or more in diameter. The composition of the forest in per cent was: hackberry 32; hornbeam (*Carpinus caroliniana*), 17; elm, 16; sweetgum, 12; persimmon (*Diospyros virginiana*) 6, mulberry (*Morus rubra*) 6; shellbark hickory (*Carya laciniosa*) 3; sycamore 2, box elder, cherry bark oak (*Quercus falcata pagodaefolia*) and green ash (*Fraxinus pennsylvanica*), honey locust (*Gleditsia triacanthos*), and bitternut hickory (*Carya cordiformis*) about one per cent each. This is in an area of extensive lumbering in 1885 and for many years thereafter. There is no suggestion of tree stumps in the area. Foresters state that walnut stumps last for about 40 years and those of most other trees perhaps half that time.

FIG. 5. The area south of Gray's Landing showing the biotic community types with the same legend as in Fig. 4b. The broken line shows the deer fence, the double lines, roads and the single lines are small streams one of which has been straightened by dredging. The tree counts for hackberry-gum were made between the deer fence and the ditch plus a small area south of the ditch.

A second area is the forest relic at Big Oak Tree Park, southeast of East Prairie, Missouri at 30 feet above mean low water, which suggests a later stage in succession. The following list shows the percentage of tree species present in an area containing 98 trees: hackberry, 21.4; mockernut (*Carya tomentosa*) 21.4; elm, 17.4 (several of these were 3 feet to 4 feet in diameter; they appear to follow the hackberry in succession); bitternut (*Carya cordiformis*) 8.2; water hickory (*Carya aquatica*) 7.2; shellbark hickory, 6.1; bur oak (*Quercus macrocarpa*) 4.1; Kentucky coffeetree (*Gymnocladus dioicus*) 3.1; swamp whiteoak (*Quercus bicolor*) 3.1; sycamore 2; box-elder 1; northern red oak (*Quercus rubra*) 1; northern hackberry (*Celtis occidentalis*) 1; flowering dogwood (*Cornus florida*) 1; mulberry and hackberry seedlings. This could be called a hackberry-elm forest and evidently is later than hackberry-gum. The area is subject to standing water in spring due to artificial drainage arrangements. The very large *Quercus macrocarpa* and swamp chestnut oak (*Q. michauxii*) are on the highest ground in the park and will be discussed later. The tree removal has not been as extensive as in Reelfoot Lake Park.

Since the undergrowth of three of the areas has been trampled, removed, or artificially flooded, it is necessary to turn to the area near Gray's Landing for consideration of the undergrowth and animal constituents. This area stands only about 21 ft. above mean low water. The type of forest present is usually about 30 ft. above this point, which suggests that the land sank in the neighborhood of 9 ft. at the time of the earthquake (1811-12). Fisk states that subsidence was 5 or 10 ft. It has not been flooded since 1912, but during the century in which it was flooded, the exposure to water was extensive.

The forest floor and some of the undergrowth are probably much more advanced in the successional series than normal for the forest type. The understory trees and shrubs are the hornbeam*,[2] hop-hornbeam spice-bush*, and pawpaw. Obser-

[2] Those species marked * persist into the climax.

vation in an area of later hackberry-gum cut in 1938 indicates that these species may appear in a very old hackberry-gum stand. The vines with foliage principally high in the trees are trumpet vine and grape. Poison ivy and Virginia creeper (*Parthenocissus quinquefolia*) showed both high and low foliage. The ivy occurs frequently as single plants at the herb level. The pepper-vine and cat-brier (*Smilax rotundifolia*)* are low foliage types. The principal midsummer herbs are Virginia snakeroot (*Aristolochia serpentaria*), Virginia knotweed (*Polygonum virginianum* L.), smooth Ruellia (*Ruellia strepens*), honewort (*Cryptotaenia canadensis*), and elephant's foot (*Elephantopus carolinianus.*)

There is a distinct vernal herbage, usually well-developed by mid-April, composed of fleabane (*Erigeron* sp.), rough bedstraw (*Galium asprellum*), jewel-weed (*Impatiens biflora* Walt.), and water-leaf (*Hydrophyllum canadense*).

This stage marks the beginning of a group of animals generally distributed in the deciduous forest. The spiders and harvestmen illustrate seasonal differences. The harvestmen (*Leiobunum cretatum* B. and C.), adults of the orb-weaver spider (*Mangora maculata*), and the crab spider (*Misumemops asperatus*) are abundant in early July and nearly absent in April and September. The jumping spiders (*Thiodena sylvana* and *Paraphidippus marginatus* Wlk.), the nursery web spider (*Pisaurina mira*), and the irregular webbed spider (*Dictyna foliacea*) were present only in our early September collections, while the water margin spider (*Dolomedes sexpunctatus*) and *Tetragnatha* were found in the woods only in spring.

A noteworthy spring phenomenon is the emergence from hibernation in April of six species of the leafhopper (*Erythroneura*) which usually are found in greater numbers on the highest ground. The shrubs and herbs on April 15, 1944 supported large numbers of leafhoppers per estimated local m^2 (figures in parentheses). Shrubs yielded *Erythroneura vitis* (143), *E. vitis corona* mixed with some *E. tacita* (210), and *E. infuscata* (32). Collections from the herbs at the same time gave *E. vitifex* (152), *E. calycula* mixed with some *E. tricincta* (83), *E. aclys* (10), and *E. vitis corona* (11).

The following invertebrates appeared in this stage; these are not regularly found in the earlier stages but continue in the later ones.

(1) Snails: *Mesodon thyroidus* Say, *Heplotrema concavum* (Say), *Triodopsis notata* Desch., *Stenotrema hirsutum* (Say) and *Mesomphix perlaevis* (Phils.). *M. perlaevis* is largely limited to the area of the tuliptree oak forest.

(2) Millipeds: *Aniulus venustus* (Wood), *Pseudopolydesmus hubrichi* (Cham.) and *Cleidogona caesioannulata* (Wood).

(3) Spiders: Several of those listed above and *Hahnia flaviceps* Em. which is a small spider of the ground surface.

(4) Beetles: *Pseudoamphasia sericea* and *Pterostichus profundus* Say and *Notoxus bicolor.*

(5) Ants: *Camponotus castaneus* (Lats.) and *Aphaenogaster fulva* Rog.

(6) Vertebrates: Amphibia and reptiles: *Plethodon glutinosus, Ambystoma microstomum, Hyla versicolor, Bufo americanus,* and *Akistrodon mokasen,* the copperhead.

There is a large series of permeant birds and mammals. These are the species which live in or wander through a large part or all of the seral stages. Such species have habitat preferences especially in regard to breeding. Most species also show some preference outside the breeding season.

As to the mammals, there are no population data available. Our observations have been limited to a few opossums, and raccoon signs. The white-footed mouse (*Peromyscus leucopus*), the golden mouse (*Peromyscus nuttalli*), and the short-tailed shrew (*Blarina brevicauda* (Say)), have been trapped. From observation records, the gray squirrel and fox squirrel are present throughout the sere including the cottonwood. A population migration estimated at 500,000 gray squirrels was described by Seton (see Bennitt and Nagel 1937). It developed on Island No. 20 opposite Tyler, Mo. where they were first noted. The forests on this one-time island were probably cottonwood and hackberry-gum at that time (1914). Squirrels are more abundant and regularly noted in hackberry-gum than in the earlier stages. The large mammals that are more migratory such as the deer, elk, black bear, and wolf are gone from the area but none of these appear to have shunned the flood plain. There is good evidence that bear and elk had a preference for the flood plain or areas adjacent to large rivers. (See Crockett 1834, Wailes 1854, Rhoades 1896.)

The following differences between the hackberry-gum and the later stages were noted in April, 1947; ten times as many millipeds, five times as many white earthworms (Euchytraeidae), nine times as many centipedes, and four times as many staplylinids were taken in the elm-hackberry as in the later stage. All of these differences perhaps resulted from the greater soil moisture. The herbs and shrubs, because of their undeveloped state, contained almost no insects or spiders. Leafhoppers, which were just emerging from hibernation, were wanting.

3. Floodplain oak-hickory communities

This is probably a series of successional facies requiring a period of one to two centuries at a particular latitude, for completion. The occurrence of oaks in this floodplain area is roughly in the order numbered. They may be classed as early (E), intermediate (I), climax (C): (1) *Quercus falcata pagodaefolia* (E); (2) *Q. palustris and Q. lyrata* (E); (3) *Q. macrocarpa* (E); (4) *Q. falcata* (I); (5) *Q. michauxii* (I); (6) *Q. shumardii* (I); (7) *Q. velutina; Q. alba* (C); (8) *Q. muehlenbergii* (C).

The hickories appear in the order given below with the same markings used: (1) *Carya laciniosa** (E) (* = not a primary dominant, ** = only scattered trees); (2) *C. illinoensis*** (E); (3) *C. cordiformis* (I); (4) *C. glabra* (I and C). These suggested relations probably do not apply north of 36° 40′ N or south of 35° N. Studies were made in the loess bluffs and ravines especially around Pawpaw Creek and on the upland several miles to east, and at South Fulton, Tenn.

The highest portion of the ridge near Samburg, Tennessee contains a predominance of oaks and hickories. This area is at about 38 feet above mean low water at Gage L W 875 L. due east of the area of study.

The relic which is being broken into home sites was sampled at several points in 1948 and in 1949, to make about one hectare in each case and the proportion of the species in 100 trees was in per cent estimated to be: cherrybark oak, 65; pin oak (*Q. palustris*) 17; Shumard oak, 5; black oak (*Q. velutina*) 4; white oak (*Q. alba*) 2; overcup oak (*Q. lyrata*) 2; bur oak (*Q. macrocarpa*) 2; southern red oak (*Q. falcata*) 2. The cherrybark oak outnumbers all other trees on the ridge even in transects across it as noted above. A few available sections indicate that they are about 50 years old. The hickories were shellbark (*Carya laciniosa*) whch appears to be most abundant with bitternut (*C. cordiformis*) a little less numerous. The oaks made up more than 50% of the stand and the hickories between 15 and 20%; the remaining species were black gum, sweet gum, American elm, winged elm, and sycamore. This indicates a phase in the development of this stage. The list of chief associates in type No. 80; (Putnam and Bull 1932) includes elm (one elm stump indicated an age of 145 years for a 24″ tree), winged elm, sweet-gum (one 20″ stump indicated a 70 year age).

The undergrowth included in addition to that found in the earlier stage, red bud and bittersweet (*Celastrus scandens*). Herbs were few—chiefly two species of *Polygonum*.

A private park (Dawson Park) near the northeast corner of New Madrid about 33 ft. above mean low water contained 43 trees. One notable tree, a bur oak was 77″ in diameter. A bur oak stump near Reelfoot Lake, 30″ in diameter, had 75 rings which would make the estimated age of the 77″ tree about 200 years. (A somewhat larger tree, 83″ is in Big Oak Tree Park.)

The Dawson Park trees, except the large one, are listed with the first figure showing the number followed by the average diameter: bur oak 25, 24″; sweetgum 5, 22″; black walnut (*Juglans nigra*) 4, 37″; persimmon (*Diospyros virginiana*) 2, 24″; elm 3, 43″; shingle oak (*Q. imbricaria*) 3; bitternut hickory 1.

In a small area of about one hectare one mile southwest of Gray's Landing (Fig. 5) containing 37 trees (12″ or more dbh): hackberry 24%; sweet gum 19%; southern red oak 14%; swamp chestnut oak (*Q. michauxii*) 19%; (12″ trees, 40-50 years old as indicated by timber theft stump ring counts); bitternut hickory 17% (12″ to 24″ trees, 40-100 years old), elm 7% and hornbeam present. The presence of *Q. falcata* is significant because it is essentially an upland tree. *Q. michauxii* which occurs only on the "second bottoms" is a fair indication of oak-hickory. Thus, both woodlands are near the oak-hickory type. The mandrake (*Podophyllum peltatum*), goose grass (*Galium aparine*), Miami mist (*Phacelia purshii*), and the red bud (*Cercis canadensis*) were not found in the nearby hackberry-gum.

On slightly lower ground, but higher than the hackberry-gum described, there are walnut trees and also shellbark hickory with the usual hackberry-gum associates. The walnut suggests a late stage of hackberry-gum.

Detailed studies of animal populations have not been made. Many of the animals of the earlier stages continue. The blue-tailed skink (*Cnemidophorus sexlinlatus*) and the slimy salamander (*Plethodon glutinosus*) appeared more abundant at this point in the sere. The former especially requires well-drained soil and relatively dry conditions.

The same snails of the genera *Euconulus, Vertigo,* and *Bifidaria* in addition to *Haplotrema concavum* (Say) appeared more abundant than in the earlier stage. The red-eyed vireo was more abundant here in spring than in the earlier stages.

4. Tulip-deer-oak biotic communities

The oaks are usually chinkapin, black, and white oak; sugar maple, and beech are also present. The last two occur near the base of the bluff in the area of study. This is Braun's (1950) western mesophytic forest.

The tulip-deer-oak communities evidently occurred on the highest flood plain near Tiptonville, but have been removed except for a few trees in

R. C. Donaldson's farm woodlot and near two adjacent houses. They are about 42 feet above mean low water at the nearest point on the river. The Donaldson trees, which suggest a late subclimax, were probably left standing because they were too large to process. The area was settled about 1840, and the age of the growing trees has not been ascertained but stumps of a few smaller trees gave some age evidence. The area of high ground (295 ft.) on which the relic occurs was cut across by a flood early in the 1900's which dug a channel and excavated a pond in what was probably a low spot between two ridges. Such scars are characteristic of flood plains.

The list of Donaldson area trees, their number and the diameter at breast height of the largest or typical ones is as follows: tulip or tuliptree (*Liriodendron tulipifera*) 2, (47", 38"); white basswood (*Tilia heterophylla*) 3, (48"), chinkapin oak, 9, (49", 30"); Shumard oak, 13, (71", 40"); cherrybark oak, 1, (49"); silver maple (*Acer saccharinum*) (51"); winged elm, 10, (20"); pin oak, 1, (38"); hackberry, 5, (20"); elm, 7, (50"); hornbeam present.

The very large Shumard oak is about 240 years old and was probably about 100 years old at the time of settlement of the area. The smaller Shumard oaks are from 125 to 150 years old as shown by 40" stumps. The tuliptrees appear to be at least 150 years old. This area has not been in the river channel for about 450 years, though the 1765 river course, as mapped, came very close to it. There have been no biotic studies of late subclimax tulip-deer-oak as only scattered trees occur. The interrelations of the plants and animals will have to be ascertained by studies in the western mesic relics if any exist.

Summary of Suggested Community Life Histories

A few facts are to be noted. The separate items of information are indicated by capital letters. All dates are referred to 1947.

A. Virgin cottonwood-willow—This was thinned in 1947 with trees 20-21 year of age. The area was in the channel of the river in 1912; 35 years are involved.

B. Older cottonwood-willow—The study station near the ferry was a sand-bar island probably with sand-bar willow in 1896 when granted to private owners by the state. It was in part washed away and deposits added at the south end. The old high part is approaching the hackberry-gum stage; some 51 years are involved.

C. Hackberry-gum—an area north and east of 39° 24′ N. 89° 31′ W. was in part in the river in 1830 and surveyed as hackberry-gum in 1912; 82 years are involved.

D. Early oak-hickory—The Mississippi River map survey of 1881 shows oak and hickory near 36° 22′ N. 89° 35′ W. (now washed away.) This was in an uncharted area two miles west of the 1675 channel involving 116 years between the two mapped surveys and an additional 135 years or thereabouts, for the river channel to move east two miles. Furthermore, it is not known what stage or type of oak and hickory was present. In this case we may assume that it was in an early oak-hickory comparable to the ones described in this paper.

E. Old oak-hickory and the subclimax tulip-deer-oak—It appears probably that in such a stage the *Quercus falcata pagodaefolia, Q. lyrata,* and *Carya laciniosa* would have largely disappeared while *Q. macrocarpa* would be present but very large and old. It is evident that 75-100 years would be necessary to eliminate the early hickories and *Q. falcata pagodaefolia* which is fast-growing and short-lived. Numerous Shumard oaks and swamp chestnut oaks would mark a stage. At about this time seedlings of tuliptree (*Liriodendron tulipifera*), the white basswood (*Tilia heterophylla*) and the chinkapin oak (*Q. muehlenbergii*) appear. They are now present at the Donaldson woodlot, and in the upland forest to the east within the study area (Fig. 1).

F. To complete a fair approximation of the western mesophytic forest of Braun (1950), probably an additional 150 years would be necessary which would be characterized by the addition of much white oak (*Quercus alba*), red oak (*Q. rubra*), sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), chestnut (*Castanea dentata*) and cucumber magnolia (*Magnolia acuminata*). It is assumed that this would require 150 years more. The Tiptonville area east of town is 305 feet above mean gulf level and has had no channel through it for an indefinite period. This may be old enough for the typical climax forest to enter.

Long Submergence Habitats and Communities

This type of habitat is associated with excessive water and occurs at the White River National Wildlife Refuge near St. Charles, Arkansas. Twenty-five ft. is regarded as a flood stage. Ordinarily the river's rise reaches or passes 6 ft. above flood stage two or more times during the average summer. In 1943, the spring flood stood at 35.4 ft. The central portion of Big Island in the White River National Wild Life Refuge has a marginal ridge on much of its circumference. The center is low and is flooded at a medium state of the river. The timber here included overcup oak (42%), water hickory and bitter pecan (26%), red oak (probably cherrybark) (11%), green ash (11%),

hackberry, elm, etc. (10%). There was mention of Nuttall oak also. (Information from W. E. Houser of the Anderson Tully Lumber Co., Memphis.) This is the Overcup oak-Water hickory type of Putnam and Bull (1932).

In early July 1943, the center of the island was just coming out of the water after two months submergence. There were few or no shrubs. Clearweed (*Pilea pumila*) was growing on logs that had floated during the flood condition. In the soil, the crayfish (*Procambarus blandingi acutus* (Gerard)) were numerous. On the ground carabid beetles (*Loxandrus erraticus*) were common. They must have passed the flood period on tree trunks or on logs. The logs and the herbs growing on them were inhabited by at least 18 species of animals. Ants found in and on the logs were: *Camponotus herculeanus pennsylvanicus* (Degeer), *Crematogaster lineolata* (Say)—a full colony, and *Aphaenogaster texana* Emery (var.). Sweeping the clearweed growing on the logs gave a variety of arthropods. Immature spiders of the genus *Dolomedes* were numerous and others of the genus *Theridion* present. A single adult harvestman (*Leiobunum vittatum* (Say)) was taken. Coleopterans included leaf-eating beetles of the genus *Lema* (probably *Lema sexpunctata*) and *Paria,* click beetles, represented by *Heteroderes suturalis,* and the flower-frequenting ground beetles *Lebia ornata.*

Flies of the longlegged fly family (*Dolicopodidae*) were represented by numerous green *Sciapus,* the Anthomiidae by *Coenosia,* the fungus gnats (*Fungivoridae*) by *Fungivora* sp. Leafhoppers were present and these and the flies are suitable food for the predatory damselbug *Nabis sordidus* which accompanied them. The most surprising thing was the presence of four individuals representing three genera of ichneumonid parasites (*Panargyrops insula* DeGant (2), and *Cryptus ultimus* Cr. (1)), and one brachonid (*Meteorus*).

On the west side of the mainland adjacent to the Big Island Chute, the water was leaving some of the area on July 8. The shrubs and seedlings were without leaves on the lower two feet of their stems in some areas; in others on higher ground they were beginning to appear. The recognizable shrubs included supple jack (*Berchemia scandens*), Missouri gooseberry (*Grossularia missouriense*). Trumpet vine and muscadine grape (*Vitis rotundifolia*) were present, but not abundant. The forest was second growth of four species of oak, hackberry, and sweetgum.) Hackberry was most abundant. Studies of the invertebrates of the shrubs indicated that there was a sharp segregation of the common species of insects and spiders present. Some were restricted to high level shrubs with a full set of leaves and others were restricted to those with a partial set of leaves.

Raccoons are usually abundant. Twenty thousand skins were taken adjacent to the refuge in the 1942-1943 trapping season. The refuge manager (Burton S. Webster) stated that raccoons have a liking for cypress communities and withstand flooding well. On the other hand, skunks and opossums cannot live in flooded areas and move in and out only to minor degrees. However, deer and bears move in and out rather freely with changes in water level. Both are nearly extirpated from the Mississippi's southern floodplain. There is no adequate knowledge of squirrels. Mice and shrews were present. They can move in and out with the changes in water level.

Big Island is an area of an immense flow of water. Its forest community cannot control the habitat. It accordingly will probably remain in much its present condition for an indefinitely long time as sort of an edaphic climax, with trees of the type now present replacing themselves in openings. Whenever less hydric trees seed in during periods of low rainfall, they will likely be drowned out in the succeeding period of high rainfall 10 to 20 years later. Striking changes in community composition will require intervals measurable in 500 to 1000 year periods rather than centuries.

Another relatively long submergence forest area is west of the Mississippi in the Little River drainage, and is low and has not received deposits fast enough to build up above frequent floods. The area of the Little River drainage west of the meander belt opposite Tiptonville and Darnell Point is lower than the area near the Mississippi River. Putnam (personal communication) states the original forest farther downstream was sweetgum-bottomland oaks with *Q. michauxii* on the ridges. Putnam and Bull (1932) state that this is No, 82 of the type list (Hawley 1940). This type occurs commonly on high clay flats and low clay or loam ridges throughout the first bottoms. The soils are usually silty or loamy and where a clay top soil occurs, it is usually underlain by a sandy or loamy subsoil. It is found rarely to occasionally in second bottoms and in very shallow swags and drains.

The predominant tree is the sweetgum. Its chief associates are water oak (*Quercus nigra*), Nuttall oak (*Quercus nuttallii*), elm, willow oak (*Quercus phellos*), hackberry, and green ash. The minor associate list covers many of the common flood plain trees—honey locust, southern cottonwood, red maple, persimmon, Shumard oak, red mulberry, sycamore, water hickory, hawthorn, box elder, white ash, etc. (Putnam and Bull 1932).

Some areas in and near the territory covered by Figs. 4a and 4b may have been intermediate between the long submergence and short submergence types. The most noteworthy one of very slow deposition of silt is north of Island No. 10. This same type of land extends north and northeast for a considerable distance. Only a little of it is cultivated. The trees along parallel 36° 40′ N. from 4 to 7 miles east of LaForge, Mo., and at Big Oak Tree State Park have been examined. The communities that formerly occurred here lie just down stream from the converenge of the waters of the Mississippi, greatly increased by the Missouri and the Ohio which is nearby augmented by the Cumberland and Tennessee. In rainy periods this means an immense flow of water in the Mississippi but the land surface is relatively higher than at Big Island hence the submergence has been much less. However an examination of cutover lands east of LaForge, Mo. does not justify assumming any difference from the usual mature hackberry-gum. It is evident that the trees concerned will tolerate a rather wide range of submergence. It is further noteworthy that in the LaForge area there is a considerable difference in the abundant native tree species as compared with the region south of Memphis.

It appears that a forest something like hackberry-elm or hackberry-gum had existed in these lower areas during many hundreds of years of slow deposition, very slowly changing to a gum-oak with bur oak on the higher ground. This is suggested by the enormous bur oaks and less frequent very large swamp chestnut oaks remaining in the higher ground after clearing. North of Island No. 10, these two types are mapped as oak-hickory and hackberry-gum, although the composition is conceived as possibly different from the types as discussed in the sere of rapid deposition areas. Earthquake uplifts such as those around Tiptonville probably favored the development of climax.

The Aquatic Sere

Shaver (1933) and Gersbacher and Norton (1939) have described the aquatic sere. The latter carried it to the hackberry-gum stage which is the point of convergence of the aquatic and alluvious seres.

1. Small flood plain ponds

Flood plains are marked by numerous flood erosion scars which persist as small ponds. They are commonly initiated by water whirling around masses of fallen trees. They are sometimes connected with the river at high water. A small pond (section of borrow pits) of about 25 acres was scraped bare in heightening a levee two miles S. W. of Markham in 1934. It contained water at least when the river was much above mean low water. Black willows of noticeable size appeared first in 1937 followed by swamp cottonwood (*Populus heterophylla*) and water locust (*Gleditsia aquatica*). The trees were 15 to 20 feet tall in 1949 and the substratum 15 years old.

2. The development of cypress in swamps

The germination of cypress seed and the early growth of the seedlings in a state of nature has been too little investigated. It is evident however that two or more years of drought are essential for germination and establishment. Demaree (1932) found that seed must sprout when not submerged and the seedling must not be submerged. This means that most of them make a successful beginning in the drought periods such as in the early 1930's. It was in that year that the lake was lowest and the first seedlings were seen. By 1936 they were 1 to 3 meters high.

The consideration of the aquatic sere begins with decadent stands of giant cutgrass (*Zizaniopsis milacea*) which probably required 100 to 150 years to reach decadence in large river oxbows (no such cut-offs in historic times) to become the principal seed bed for large cypress areas. The tree lives to be very old (300 to 400 years). Fisk (1944) shows a 1200 A.D. channel (Fig 2) which curves around the southwest shore of the deep portion of the lake. There are suggestions of the existence of a narrow water-filled remnant of the resulting oxbow at the time of the earthquake. It is now evident near the present shore at Boyette's boat landing (By, Fig. 4b). There is the remnant of a curved row of sunken but living trees in about 7 feet of water about 200 feet off shore with no sunken trees between the row and the shore. It can be assumed that this open space contained no trees at the time of the earthquake. The row at the point of observation is broken at x where it curves farthest from the shore and subsidence was greater and the water deeper. Beyond the row is what appears to be a large area of cypress stumps still two or more feet in diameter and standing in 15 feet of water over most of the areas as mapped for the large channel. The row of living cypress was probably about 10 inches in diameter at breast height when sunk. They have developed large thickenings just below average water level with suggestions of roots and have grown very little. It was 600 years from the time the channel was formed to the earthquake and the development of a good stand of large cypress, perhaps 150 to 200 years old. If 200 years is allowed for the oxbow to have been cut off, then 200 more must have been consumed in develop-

ment of cutgrass, willow etc. such as provided conditions for the germination of seed in the low water period of the early 1930's. Seedlings not appearing in the cutgrass-willow area came up through a heavy litter of twigs and leaves in shallow water near shore.

According to Fuller (1912), the shallower portions of the lake were occupied by stubs of walnut, ash, oak, elm and mulberry which could be recognized in 1905. This suggests an oak-elm-ash forest. Such forests occur in wet areas in so-called first and second bottoms (Putnam and Bull 1932: 45). Part of this area is mapped as an 800 A.D. channel (Fisk 1944). With 1000 years to develop, part of it could have succeeded cypress. The walnut taken out for furniture would fall on the flood-plain associated with the 800 A.D. channel. It was removed at point W of Fig. 2 in the 1880's.

The Construction of the Vegetation Maps

Small areas of all the communities noted were available but disturbed. The extension of the mappings over areas which have been destroyed is based upon: (a) the age of the deposit and (b) its height above mean low water which does not apply in all cases due to earth movements. Mean low water varies from approximately 266 feet above mean gulf level at the northeast corner of the map to 248 feet at its southwestern corner, a difference of 18 feet (Table I). This limits the use of contour lines above mean gulf level which can be used only in connection with mean low water at the nearest river gage.

The relations of age of deposits need illustration. The relation to water levels has been followed on the preceding pages starting with the area west of the river in Fig 4a, subclimax tulip-deer-oak is assumed on the ridge west of New Madrid at 40 to 44 feet above mean low water and on the smaller area northeast of Marston and to the left of I in the channel. There are no records of river action here for several hundred years. The site of New Madrid (N. M.) at 30-35 feet above low water was evident in oak-hickory at the time of the earthquake and is on old deposits. The mapped piece of subclimax tulip-deer-oak, southeast of Marston and at the left of II stands on ground 41 to 45 feet above mean low water. A high area reaches northeast nearly to the river. The east half of this area was washed away in 1820 and built back again by 1947. It is not possible to assume that the forest is late subclimax after only 127 years (Table II.) Thus, the east half of the area is mapped as hackberry-gum while the high ground to the west above 295 feet is mapped as late subclimax. This is because there is no evidence that it has been disturbed by the river for more than 450 years. The cypress-ash immediately to the left is shown on the levee and river charts of 1885. The cypress-ash type corresponds to the tupelo gum type No. 95 of the Society of American Foresters in combination with No. 94 "Southern Cypress."

Table II. *Schedule of community development*

Item in text	Years in period	Description of areas and processes	YEARS Added	YEARS Total
A	35	Building of sand bar to 5 feet above M. L. W.; April-May; water-level suitable for sand-bar willow	2-4	2-4
		Growth of sand bar willow. Deposition of 10-20 feet of sand for seeding of cottonwood and willow. Elimination of total submergence of willows	11-13	13-15
		Growth of cottonwood-willow through equal growth period of the two	19-21	34-36
B	51	Area assumed ready for cottonwood-willow at beginning. Less 21 gives 30 years of (a) elimination of willow dominance, (b) development of maple-box elder under cottonwood, (c) entrance of hackberry and gum	28-30	64-66
C	82	Less 65 years; 17 years eliminates cottonwood dominance; beginning of hackberry or gum dominance	16-18	80-84
D	116 + 134	175 years for entrance of elms, early oaks and hickories. Subordination of hackberries and gums. Entrance of intermediate oaks and hickories	175-180	250-270
E	No data	First phase; elimination of early oaks and hickories	80-100	340-360
	450	Second phase; 100 years entrance of tulip and oak species	60-100	430-450
F	....	Entrance of some remaining tulip-oak forest species	150-170	600-620

In the aquatic sere it must be noted that "open water and stubs" of the legend is misleading because many of the stubs are living cypress trees, many dwarfed by submergence, but some full-sized.

Acknowledgments

General use has been made of various maps, viz:—the topographic maps of the U. S. Geological Survey and the Army Engineers, and the Stream Channel map of the Mississippi River Commission, C. L. Baker's map of Reelfoot Lake based upon aerial photographs of the Soil Conservation Service, and the survey of the State Park by the Tennessee Division of Geology. Baker's personal soundings of the waters of the lake were especially valuable. Mr. John Steenis also supplied important information. Mr. E. A. Peacock of Tiptonville gave valuable information

regarding the flood of 1937 and also valuable personal assistance. The writer is indebted to Dr. H. N. Fisk and Dr. R. E. Shanks for assistance with the manuscript.

Mr. R. C. Donaldson of Tiptonville did numerous services in addition to his article in the Lake County Banner. He supplied information as to the history of various land areas, new and old, location and dates of logging operations, etc. Much of his information was from his law practice in litigations over titles to new land built up by the river. He also accompanied the author on several study trips.

The identification of plants in the field was made by Mr. E. Cypert, forester in the U. S. Fish and Wildlife Service, who cruised the hackberry-gum and early oak-hickory south of Gray's Landing with the aid of Mr. John Steenis in April 1947. Mr. Julius R. Swayne of the Southern Illinois University Museum made extensive identifications in 1948, aided by W. M. Bailey. Identification of White River herbs and shrubs was by D. M. Moore; those from Reelfoot Lake, by G. N. Jones of the University of Illinois. Thanks are also due Mr. John N. Putnam of the Southern Forest Experiment Station for assistance with the communities.

The identifications of animals were made or verified as follows: Ants—M. R. Smith; Amphibians—Hobart M. Smith; Centipedes—R. S. Chamberlin; Hemiptera—H.M. Harris; Homoptera—R. H. Beamer; Mollusca—H. van der Schalie and Glenn R. Webb; Millipeds—Hugh Hanson; Reptiles—A. R. Cahn. Various orders of insects present in small numbers were identified by the staff of U. S. National Museum. This valuable contribution is greatly appreciated.

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THE PLACE OF GRASSLANDS IN THE EARTH'S COVER OF VEGETATION

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Grasses in nature's plan of world development have served a most constructive purpose. They have rapidly occupied new or raw lands and lands depleted of their forests by cutting or by fire or both. Even excessive grazing has been followed by less palatable and nutritious grasses. They have also enriched the soil material to produce our grain lands, some of which have held their fertility even after years of cultivation.

Forests and forestry have received much more attention than the grasslands and the problems connected with them. Agrostology has been mostly systematic study of the species rather than the combined ground cover. Six International Grassland Congresses have been held but they have dealt largely with the animal husbandry phases of the problem and with grasslands established on lands naturally occupied by deciduous forest. Even most of the studies of range lands deal with them from the standpoint of domestic livestock. Much of the work comes under the heading, Grassland Agriculture. This is the dominant theme, and the livestock industry will influence work along this line. However, the lands of the world on which we largely depend for our continued nutrition were made and enriched by the grasslands. We have stopped most of this constructive process on our prairies. Cultivation is a method of making immediately available to the plant the nutritive materials of the soil. The prairie grassland builds it back. About 75 years ago, Professor T. J. Burrill planted forest trees on the natural prairie at Urbana, Illinois. After 70 years of forest growth, Simpson found that the forest increased the acidity, decreased the organic matter, lowered base exchange, and in every way moved the rich dark prairie soil in the direction of the gray-brown podzolic soils of the deciduous forest region adjacent to the grasslands (Simpson, C. H., "Some effects of seventy years of forest vegetation on the grassland soil." M. S. Thesis. University of Illinois, Feb. 1931). It would seem reasonable to expect that after the forest had been driven back by fire, the grasses had taken over and built up the gray-brown podzolic soils by increasing the organic matter and the exchangeable bases and had moved the soils in the direction of the chernozems. A similar action make take place when the lateritic soils under the tropical rain forests are occupied, following the destruction of the forest by cutting or by fire or both, by the grasses of the high grass savanna if the grasses are not too frequently burned.

Only general estimates can be made of the area occupied by the different types of vegetation on a world basis. Using the best material available, the vegetation was mapped on equal area maps and the areas estimated. On this basis the areas showed the following values for the major divisions first used by Schimper.

		Per cent	
Division	*Square Miles*	*Land Area*	*Earth Area*
Forest	21,970,000	42	11
Grassland	12,570,000	24	6
Desert	17,430,000	34	9
Total	51,970,000	100	26

In addition to the area above there are

Water	139,150,000	71
Ice Caps	5,830,000	3
Total	196,950,000	100

Forests are rather closely correlated with climatic conditions, and are confined largely to the pedalfer soils where the subsoils are moist and the soils are leached.

The grasslands are of two types: (A) Those determined largely by climatic conditions and on pedocal soils, unleached and with dry subsoils, and (B) those which have replaced forests destroyed by cutting or by fire or both, or maintained against forest development by conditions favoring fire.

Under deserts are included the hot dry deserts, the alkali deserts, and the tundra or cold deserts.

Sclerophyll brushlands or the Mediterranean type classified with the forests are a fire type. They are generally at the dry edge of the forest area, often on a pedocal soil and inflammable during the dry warm part of the year. It is doubtful if any areas of this type can be found that have not been burned repeatedly. Burning does not kill out this type but perpetuates it.

The term "plant community" is applied to any grouping of plants and since it is not limited is a perfectly safe term to use to designate a clump of shrubs or the great band of tropical forest. Plant

communities have been studied and interrelated and an elaborate system designated by such technical terms as formations, associations and societies. In studying any one of these, it is desirable to recognize criteria for comparison. Very elaborate systems have been proposed but a simple system based on the historical development of the subject is limited to four criteria: (1) physiognomy or the general appearance, (2) floristic composition, (3) succession or the stage of development, and (4) response to environment or a consideration of the habitat.

The natural vegetation can be grouped into about 17 groups. These I would regard not as formations but as groups of formations.

	Area in sq. miles	*Per cent*	*Per cent*
Forests			
Tropical Rain Forest	3,800,000	17	
Temperate Rain Forest	550,000	2.5	
Deciduous Forest	6,500,000	30	
Coniferous Forest	7,600,000	35	
Dry or Monsoon Forest	2,000,000	9	
Thorn Forest	340,000	1.5	
Sclerophyll Brushland (Mediterranean Type)	1,180,000	5	
Total Forests	21,970,000	100	42
Grasslands			
High Grass Savanna	2,800,000	22	
Tall Grass Savanna	3,900,000	31	
Tall Grass	1,580,000	13	
Short Grass	1,200,000	10	
Desert Grass Savanna	2,300,000	18	
Mountain Grassland	790,000	6	
Total Grassland	12,570,000	100	24
Deserts			
Desert Shrub and Desert Grass	10,600,000	61	
Salt Desert	30,000	0	
Desert (Hot and Dry)	2,400,000	14	
Tundra (Cold)	4,400,000	25	
Total Desert	17,430,000	100	34

It is impossible to draw sharp distinctions at the borders of these regions. Grasses play a very important place in many of the forests and desert areas. In the Coniferous Forests there are many grassland areas. In such divisions as the spruce-fir forests and along the dry sides of such forests as the juniper-pinyon and in the western and southeastern pine forests. It would seem reasonable to consider one-tenth of the Coniferous Forest as grassland. This would be an area of 760,000 square miles. The Monsoon or Dry Forest can with difficulty be separated from the Tall Grass Savanna and about one-fourth or 500,000 square miles may be considered grassland. Desert Shrub and Desert Grass in many places is nearly pure grassland and one-tenth of the area or 1,060,000 square miles may be regarded as grassland. The Tundra is largely grassland and at least half or 2,200,000 square miles can reasonably be added to the grasslands. With these transfers the earth cover would be about as follows:

Forests	21,970,000 sq.m.	
Loss to Grasslands	—1,260,000	
Total	20,710,000	40 per cent
Deserts and Tundra	17,430,000	
Loss to Grasslands	—3,260,000	
Total	14,170,000	27 per cent
Grasslands	12,570,000	
Gain from Forests	+1,260,000	
Deserts	+3,260,000	
Total	17,090,000	33 per cent
Total Area	51,970,000	100 per cent

Many grasslands have been increasing at the expense of adjacent forests following cutting or fire or both. The High Grass Savanna is gradually replacing the Tropical Rain Forest as a result of clearings and of fire. The Dry Forest is likewise giving way to the Tall Grass Savanna, and the Temperate Rain Forest to the Mountain Grassland. The Tall Grass or Prairie is not a true grassland from the standpoint of climate or soils and if not burned would give way to Deciduous Forest. If these considerations are accepted the potential forests would be as follows:

Forests	Actual	Potential	Total	Per cent
Tropical Rain Forest	3,800,000			
+High Grass Savanna		2,800,000		
			6,600,000	22
Temperate Rain Forest	550,000			
+Mountain Grassland		790,000		
			1,340,000	4
Deciduous Forest	6,500,000			
+1/2 Tall Grass		790,000		
			7,290,000	24
Coniferous Forest	7,600,000		7,600,000	25
Dry Forest	2,000,000			
+Tall Grass Savanna		3,900,000		
			5,990,000	20
Thorn Forest	340,000		340,000	1
Sclerophyll Brushland	1,180,000		1,180,000	4
Total	21,970,000	8,280,000	30,250,000	100

Much of the forest land could under certain conditions become grasslands. An estimate of the potential grassland would be as follows:

Grassland	Actual	Potential	Total	Per cent
High Grass Savanna	2,800,000			
+Tropical Rain Forest		3,800,000		
			6,600,000	25
Tall Grass Savanna	3,900,000			
+Dry Forest		2,000,000		
			5,900,000	23
Tall Grass	1,580,000			
+1/2 Deciduous Forest		3,250,000		
+1/10 Coniferous Forest		670,000		
			5,500,000	21
Short Grass	1,200,000		1,200,000	5

Desert Grass Savanna	2,300,000			
+1/10 Desert Shrub and Desert Grass		1,060,000		
			3,360,000	13
Mountain Grassland	790,000			
+Temperate Rain Forest		550,000		
			1,340,000	5
Tundra (1/2 of total)	2,200,000		2,200,000	8
Totals	14,770,000	11,330,000	26,100,000	100

These considerations may be summarized as follows:

Type	As Mapped	%	Actual Occupancy	%	Potential	%
Forest	21,970,000	42	20,710,000	40	30,250,000	58
Grassland	12,570,000	24	17,090,000	33	23,900,000	46
Desert	17,430,000	34	14,170,000	27		
	51,970,000	100	51,970,000	100		

About half (57%) of the land surface of the earth is covered with pedalfer soils. In these soils, the moisture is in excess of the demands of the vegetation and water passes down through the soils leaching them and moistening the subsoils down to the water table. About half (43%) of the land surface of the earth is covered with pedocal soils. In these soils, moisture is held in a surface layer and usually completely absorbed by the growing vegetation and none passes down into the sub-soils which remain dry.

As a rule, forests are found on pedalfer soils and can only succeed on the very best of the pedocals. Grasslands are confined to largely to pedocals and when growing on pedalfers are not strictly climax but except for the aid of clearing, cutting, or burning of the forest growth would be replaced by trees or brush.

If one excludes alluvial bottom lands, the most productive soils are built up under grasslands on the moister side of the pedocals.

A NEW PINE FROM THE CRETACEOUS OF MINNESOTA AND ITS PALEOECOLOGICAL SIGNIFICANCE

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Fossil records of the Pinaceae are much less numerous in the northern hemisphere than those of the Taxodiaceae. Their relative scarcity seems not so much an indication of sparse occurrence in the forests of the past as a result of factors limiting their entrance into the sediments of Cretaceous and Tertiary basins. With some notable exceptions, such genera as *Pinus, Abies,* and *Pseudotsuga* have their greatest abundance on upland slopes at the present time. By contrast *Sequoia* and *Taxodium* are largely confined to lowlands, and *Metasequoia,* although a highland tree, is restricted to valleys. Not only are these lowland and valley trees in a more favorable situation to enter the sedimentary record, but their habit of shedding shoots with numerous attached leaves provides a more conspicuous foliage sample than the single needles of *Abies* and *Pseudotsuga* and the fascicles of *Pinus*. *Metasequoia* and *Taxodium* drop their foliage annually and the crop is a large one because of the great size of the trees; in the Tertiary record of North America, in which these two genera are more abundant than any other conifers, leafy shoots are the most numerous units of the plant represented. If *Pinus, Abies,* and *Pseudotsuga* lived on slopes remote from sites of deposition in the past, as most trees of these genera live today, we should expect to find their readily disseminated seeds more common as fossils than their leaves and cones; this is actually the case in most of the Tertiary floras in which they are found.[1] So it seems probable that the abundance of certain of the Taxodiaceae as fossils is to a large extent due to factors which favored their entrance into the sedimentary record, and does not indicate that they were more numerous or widespread than the Pinaceae during Tertiary time. Authentic records of the genus *Pinus* in the preceding Cretaceous period are comparatively few, and have rarely received more than superficial attention. This study of well-preserved cones from the Dakota sandstone of Minnesota is the first to establish the presence there of a pine closely related to the living red pine, *P. resinosa* Aiton, the Minnesota state tree. During intervening scores of millions of years there must have existed trees representing on the one hand the descendents of this Cretaceous pine, and on the other the more immediate ancestors of the red pine; but there is

[1] Pine pollen is reported by Wodehouse from the Eocene Green River formation of Colorado and Utah (1933: 487-488), and by Jane Gray, graduate student at the University of California, from the Eocene Claiborne formation of Alabama; there is no other record of *Pinus* from these deposits.

no known Cenozoic record of a fossil pine of the *P. resinosa* type.[2] This gap in the history of the red pine is one of the many examples of the incompleteness of the fossil record, and serves to emphasize the limitations of our knowledge of past vegetation.

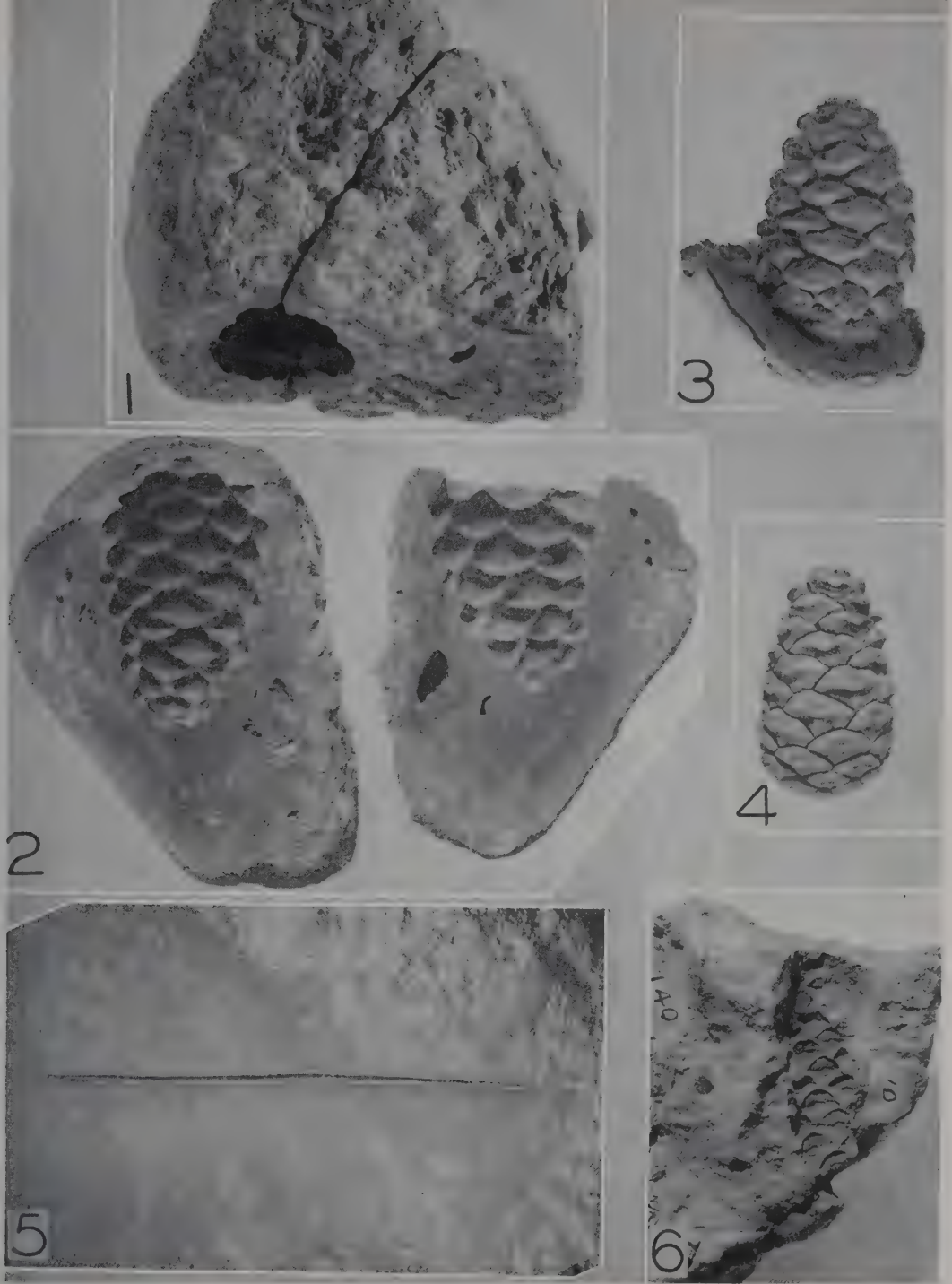
A total of 86 species of *Pinus* have been recognized in North America, in deposits ranging in age from Jurassic to Pleistocene. There is much question regarding the generic status of foliage specimens referred to *P. nordenskiöldi* Heer from Jurassic deposits in Oregon (Fontaine 1905: 131, Pl. 35, Figs. 10-17) and in California (Fontaine 1900: 362, Pl. 45, Fig. 3). Heer's original specimens of *P. nordenskiöldi,* as figured from Spitzbergen in Flora Fossilis Arctica (1877: 45, Pl. 9, Figs. 1-6), represent dissociated fragments which may represent pine needles, but his discussion and illustrations are not convincing. In view of the recently reported occurrence of *Sequoia* from the Jurassic of Manchuria (Endo 1951: 228-230, Figs. 1, 2), there would seem to be no reason why *Pinus* may not also have lived during this period. Seventeen species have previously been recorded from Cretaceous deposits, including several represented by fragmentary foliage of uncertain status; there are 50 species, not all of which are in good standing, from the Tertiary, and 19 species from the Pleistocene. Wood, foliage, cones, seeds, and pollen are preserved as fossils, with foliage and seeds most commonly encountered. Many of the Pleistocene species are represented by most or all of these organs or groups of organs, and it has been possible to refer them to species now living. Some of the older remains also show resemblances to corresponding structures of living species, but in no case are they sufficiently complete to establish specific identity.

I am grateful to Emeritus Professor C. O. Rosendahl for bringing a nearly complete fossil cone to my attention during a recent visit to the University of Minnesota, and for turning it over to me for study. Dr. Rosendahl has always shown a keen interest in fossil plants, and has made large collections from the shales and sandstones of the Dakota group in south-central Minnesota. This specimen was given to him by C. W. Blue a number of years ago, and was found at the pits of the A. C. Ochs Brick and Tile Company near Springfield. It represents the external mold of an ovuliferous cone whose shape has not been altered by compression, and is complete except for the base which has been broken off from the piece of rock in which it is embedded. This rock mass is irregularly lenticulate in shape, with dimensions 8 x 7 x 5 cm. (see Figure 1). It appears to represent a sideritic concretion in a sandy mudstone, a center where iron carbonate has been concentrated. One end has been broken exposing the mold of the cone within; if any of the material of the cone was ever preserved, it was no longer in the mold when the concretion, sawed in the longitudinal plane of the cone and slightly off-center, was turned over to me (see Figure 2). The suggestion may be made that this concretion represents an aggregate somewhat similar to the coal balls of the Carboniferous, in which the pine cone served as a nucleus. Like coal balls, it shows evidence of other plant fragments in its interior, but these also occur as molds from which the plant material has disappeared, rather than as petrified structures. So far as known this is the only cone discovered at Ochs Clay Pit, although on one side of the concretion there are numerous, apparently dissociated, scales which may represent the remains of a second cone. Impressions of angiosperm leaves are numerous in the layers of hard, calcareous sandstone interbedded with the clay, and have been studied in a preliminary way by Rosendahl and his students.

During the study of this cone, I have had occasion to survey previous records of *Pinus* from the Cretaceous of Minnesota and adjacent states, and have found that Lesquereux reported the presence of this genus near New Ulm, some 25 miles east of Springfield. He described, without illustration, a leaf assigned to *Pinus* species (1895: 10), and listed *P. quenstedti* Heer[3] from the same or an adjacent locality without either description or illustration (p. 22). An inquiry regarding these specimens to Dr. John W. Hall of the Department of Botany at the University of Minnesota has been most productive; he has sent me Lesquereux's original specimen of *P. quenstedti,* No. 5384, representing the impression of a leaf (see Figure 5), and a second specimen not mentioned by Lesquereux on which there are impressions and a compression of three cones apparently identical

[2] Foliage resembling that of *P. resinosa* is figured by MacGinitie (1953, pl. 18, fig. 1) as *Pinus* leaves, but there are no accompanying cones.

[3] Lesquereux also described leaves and a cone of *P. quenstedti* from the Cretaceous of Kansas, but this material is wholly unlike the Minnesota pine for the leaves are in fives, and the cone is elongate and asymmetrical (1883: 33, Pl. 1, Figs. 3, 4). Resemblance of his specimens to "the living Mexican Pines" is noted by Lesquereux; formerly known as *P. montezumae* Lambert, this pine is now considered by Martinez (1948: 260-266) to represent the Montezuma Complex (Grupo Montezumae) including a number of species of which *P. michoacana cornuta* Martinez has cones most similar to the Kansas fossil (see Martinez's Figure 213, also Shaw, 1914, Pl. 25, Fig. 222). It will be a matter of great interest if the ancestry of the Montezuma pines can be traced back to the Cretaceous period.



FIGS. 1-6. Illustrations of *Pinus clementsii* Chaney.

FIG. 1. Concretion showing the mold of a cone. Holotype. Univ. Minn. Dept. Botany, Paleob. Coll., No. C770. Ochs Clay Pit, Springfield, Minn.

FIG. 2. Concretion opened to show the cone in vertical section.

FIG. 3. Cast of the cone shown by figures 1 and 2.

FIG. 4. *Pinus resinosa* Aiton for comparison with the fossil. Cone from a tree growing under cultivation at the Institute of Forest Genetics, Placerville, California.

FIG. 5. Impression of a portion of a leaf. Paratype. x 3. Univ. Minn. Dept. Botany, Paleob. Coll., No. 5384. New Ulm Minn.

FIG. 6. Compression of a cone. Paratype. Univ. Minn. Dept. Botany, Paleob. Coll., No. C771. New Ulm, Minn.

with the cone from Ochs Clay Pit (see Figure 6); these specimens carry the New Ulm locality designation, No. 140. The specimen on which Lesquereux based his brief description of a leaf referred to *Pinus* species is not now known to be in the collections at the University of Minnesota. The recently received specimens occur in association with angiosperm leaf impressions on slabs of fine-grained limonitic sandstone.

In spite of the fact that this fossil material seems scarcely distinguishable from corresponding parts of the living *P. resinosa,* and over the long-remembered objections of Frederic E. Clements who, with many other botanists, often seemed to favor calling fossil plants by the names of living species which they resembled, I am assigning a distinct specific name to it for the following reasons:

(1) We know nothing of the wood, microsporangiate cones, and pollen of this Cretaceous pine. It is reasonable to suppose that, during the scores of millions of years since our cones were borne on living trees, there may have been changes in some of these organs or groups of organs which would provide a basis for specific distinction.

(2) From the standpoint of the historian (and all paleontologists and stratigraphic geologists are historians), it is preferable to assign a different name to a plant which is so far separated in age from the pines of our day; this emphasizes the temporal and stratigraphic distinctness of the fossil pine.

Mention of its modern affinities gives all of the advantages that would accrue from using the name *P. resinosa,* and at the same time does not commit us to an opinion, and to a record of specific identity, which cannot now be established on the basis of the material available.

My selection of a name for these fossils might have brought about another mild argument with Dr. Clements. In assigning the name *Pinus clementsii,* I am disregarding his preference for bisyllabic specific names, but if this procedure were followed consistently, no one with two syllables in his name could ever have a species named in his honor without leaving off the case ending; and that, to a classical scholar like Clements, would have been a greater sin than tri-syllaby. At any rate, if I had named this pine in honor of Dr. Rosendahl, which would also have been highly appropriate, I should have used a still longer specific name. So I am assigning the name *Pinus clementsii* in appreciation of the man who guided my early paleobotanical studies in western North America, giving me suggestions and ideas from his great store of knowledge of vegetation, both present and past.

When I brought the cone of *P. clementsii* to Berkeley, my first thought was to discuss it with Dr. Nicholas T. Mirov, Plant Physiologist of the California Forest and Range Experiment Station of the United States Forest Service, for in recent years he has made an extensive study of the living and fossil species of *Pinus.* His judgment regarding the modern relationship of our material has proved to be of great value, as indicated by the following statement which he has prepared for inclusion here: "The fossil cone you sent me apparently belongs to the subgenus *Diploxylon* (hard pines). Within the subgenus, the cone falls into the group *Lariciones* 'which represents the first stage in the evolution of the hard pines' (Shaw 1914: 51). This group consists of 12 living species; seven are Asiatic, three European, and two American, *P. resinosa* and *P. tropicalis.* The cone in question differs a great deal from the cones of the European and Asiatic *Lariciones* either in shape or in the appearance of the apophysis. A difference in shape and size is also apparent when it is compared with *P. tropicalis.* The fossil cone is indistinguishable from the cone of *P. resinosa* in its shape and especially in the appearance of the apophysis, characterized by an unarmed, delicately outlined umbo."

It is fortunate that the cones of this fossil pine and of its living relative are so characteristic, for with the exception of a fragmentary needle there is nothing else to indicate its modern relationship. The paleobotanist must often make use of fragmentary evidence in his study of Cretaceous and Tertiary specimens, for although there is occasional record of a fossil plant which is essentially complete, as in the occurrence of *Metasequoia disticha* Miki in the Pliocene of Japan (Miki 1941: 260-262), it is unusual to find more than one or two parts of any plant associated in the same deposit, and extremely rare to find them in direct attachment. Most of the conifers and angiosperms of these later floras show a close resemblance to living species; here the standard procedure is to bring together one or more parts of a plant if all of them show similarity to the corresponding parts of a living species, and to assign them all to a single fossil species even though they do not occur in direct attachment. Where only one part of a plant is found, sufficiently well-preserved or sufficiently distinctive to make possible a generic identification, it is described as a new fossil species if nothing resembling it has previously been found. Subsequently other parts may be discovered in rocks of approximately the same age, and these may be assigned to the same fossil species if they

show similarities to the corresponding parts of a related living species.

This procedure has been followed in the study of the cones and needle from the Cretaceous of Minnesota. Future discoveries may provide a more adequate concept and may alter some of our conclusions, but such a contingency is not limited to the study of *fossil* plants. Following is the description of the material now at hand:

Pinus clementsii new species

Description.—Foliage represented by a fragment of a leaf 2.5 cm. long, complete at neither end; slightly over .5 mm. in width, tapering slightly distad; deeply concave in cross-section, subtending an angle of approximately 180 degrees. Ovuliferous cones ovoid-conical, symmetrical, broadly rounded toward the base which is missing, only slightly more gradually rounded distally to a blunt tip; maximum length (actual) 4.5 cm., (estimated) 4.7 cm.; greatest diameter 2,8 cm.; scales of the cones closed in all cases, so that the apophyses are confined within the surrounding apophyses; apophyses approximately rhombic in cross section, but more rounded above and more angular below, up to 1.1 cm. across and 7 mm. high on the uncompressed specimen, with a strongly convex surface protruding as much as 2 mm., with a distinct transverse keel, with a strong ridge extending from the umbo down to the base, and with faint, and in some cases a few strong, linear grooves radiating out from the umbo; umbos dorsal, up to 2 mm. across, mutic, broad rhombic or irregularly lenticular, surrounded by a distinct moat.

Discussion

Shape and size in the above description are based upon the uncompressed cone shown as Figure 3. The surface characters of the apophyses and umbos are best preserved on the fragmentary cone shown as Figure 6, in which compression has not only flattened the cone, but appears to have squeezed it longitudinally until the apophyses are approximately as high as they are wide.[4] Pressure applied to a cone of the living *P. resinosa* after soaking produces a similar increase in its length, and a vertical distortion of its apophyses.

These two cones, and two other fragments not figured, closely resemble those of *P. resinosa* in shape, size, apophyses, and umbos (see Figure 4). The only observed difference is that the apophyses of our best preserved specimen have stronger protuberances than those of any of the cones of *P. resinosa* examined. In one further feature, which may be only coincidental, this specimen is suggestive of *P. resinosa:* it is incomplete at the base as a result of the fracturing of the nodular mass of rock in which it is preserved; fallen cones of the living species commonly have the base missing since they tend to leave a few basal scales at the point of attachment. The possibility exists that this fossil cone also was incomplete at the time of burial, and that the position of the break across the enclosing concretion was determined by the end of its mold. The closed scales on all our cones, with their apophyses closely surrounded by those adjacent, are interpreted as indicating that they were in water at their time of entry into the sedimentary record. Cones of *P. resinosa* close their scales when placed in water (see Figure 4) even though they have been open and spreading at maturity; when removed from water, they reopen their scales within a few hours. With the exception of the specimen shown as Figure 6, the apophyses and umbos on all the fossil cones appear to have been abraded prior to burial. Modern pine cones float in water, and it seems probable that the abrasion of the fossil cones occurred while they were being transported in suspension from the place where their parent trees grew to the sites of deposition farther down the valley, as will be mentioned below.

The foliage specimen, although only a fragment, also shows characters which indicate its resemblance to the leaves of *P. resinosa,* or at least to those of a two-needled pine. At first glance it might be doubted whether so incomplete a specimen (see Figure 5) could have any bearing on the modern relationships of *P. clementsii,* or whether it could even be considered to represent the same species of pine as the fossil cones. While two needles associated in a fascicle would immediately have served to confirm the reference of our foliage and cone specimens to a single fossil species similar to *P. resinosa,* the cross-section of this incomplete leaf in itself is sufficient to indicate its binate character. As above described, it is concave, forming a sector of approximately 180 degrees, which as Shaw has stated (1914: 4) is a definite indication of a fascicle of two leaves. Examination of the foliage of all the common living American pines shows that only the two-needled species have leaves similarly concave in cross-section; of these several have leaves much more heavy than the fossil specimen, leaving *P. contorta* Dougl., *P. muricata* D. Don, and *P. resinosa* as the only living species with wholly similar leaves. No fossil cones have here been found with spines like those on the apophyses of *P. contorta* and *P. muricata,* and so the possibility of relationship to these species can be eliminated, at least so far as

[4] A thin carbonaceous film representing the remains of this cone covers several of its scale imprints. This material is now being studied by Adriance S. Foster.

cones now known are concerned. Close similarity of *P. clementsii* to *P. resinosa* appears to be established on the basis of comparisons both of the cones and of the foliage.

Physical Conditions

The absence of Mesozoic rocks of pre-Cretaceous age from southern Minnesota indicates a long expanse of time during which erosion equalled or exceeded deposition. That some of the highlands lasted through this stage of emergence in an adjacent area, or were uplifted during Cretaceous orogeny, is indicated by the coarse character of some of the sediments of the Dakota group in which the cone of *P. clementsii* was collected. (For sections, see Stauffer and Thiel 1941: 128-130). The Dakota sandstone, basal member of the Upper Cretaceous, is largely continental in origin, and represents a stage in earth history during which streams were depositing sediments on broad floodplains over a wide area between the Front Range and the Mississippi Valley. The local occurrence of poorly drained areas is indicated by thin lenses of lignite in the section at Ochs Clay Pit and elsewhere.

The vegetation of the Dakota stage in North America gives the first record of a predominantly angiosperm forest. Preceding floras of the Lower Cretaceous show still a large element of such older Mesozoic plants as the Cycadophyta and Ginkgoales, together with ferns and conifers of ancient types. But with Upper Cretaceous time, flowering plants, and to a lesser extent modern conifers, became the dominant members of the forests of the northern continents. With the exception of the pine here described, and a foliage shoot considered by Lesquereux to represent *Sequoia*, the flora from southern Minnesota is made up entirely of angiosperm leaves. These have been assigned to such genera and form genera as *Alnites, Salix, Populites, Platanus, Ficus, Laurus, Cinnamomum, Diospyros, Andromeda, Bumelia, Cissus, Magnolia, Liriodendron, Dewalchia, Juglans, Crataegus, Sapindus, Protophyllum, Aralia, Leguminosites,* and *Laurophyllum* (Lesquereux 1895: 22), but it requires only a brief survey of the illustrations to indicate that many or most of the figured specimens are at best blurred copies of the leaves of modern angiosperms, and do not show characters which permit accurate generic determinations. This is true also of leaf impressions from localities of the Dakota sandstone in adjacent states.[5] Even in the case of the much later flora from the Lance formation, the uppermost member of the Upper Cretaceous, Dorf has stated (1942: 97): "The task of allocating Upper Cretaceous species to their proper botanical genera continues to be a difficult one. Many of the Lance species are still of very uncertain systematic position. Others are believed to show only a family relationship to existing forms. Not many can be shown to have a marked resemblance to living genera." It is not until the Tertiary period that the leaves of angiosperms, often in association with seeds and fruits, can be assigned with confidence to modern genera. This being the case, the question may be raised whether the angiosperm flora of the Dakota sandstone provides any reliable basis for reconstructing the Upper Cretaceous environment in southern Minnesota. The answer can be given that whatever the systematic position of these Cretaceous leaves, whether *Alnites crassus* Lesquereux represents an alder or a *Viburnum* (which the venation and margin appear to indicate), whether *Laurus nebrascensis* Lesquereux is actually a lauraceous leaf or a member of any one of a dozen other genera and families with lanceolate leaves, there are still characters shown by the leaves themselves which suggest the physical conditions of their day. These characters of size, venation, margin and texture, while perhaps not reliably interpretable from Lesquereux's drawings, are none the less suggested by his figures, and can be readily checked by examination of leaf impressions from the Dakota sandstone. Reference may be made to numerous papers in which the principles of leaf analysis are discussed in connection with Tertiary floras (see Chaney and Sanborn 1933: 18-23), and it is clear that these principles apply equally well to the treatment of Cretaceous leaves.

An analysis of 200 species of the Dakota flora from Minnesota, Nebraska and Kansas, based upon an examination of the descriptions and illustrations of angiosperm leaves (Lesquereux 1874, 1883, 1891), has provided the data summarized in Table I. Analyses of other floras are included for comparison.

A large majority of the Dakota leaves have entire margins and thick texture; these are characters found in many leaves of the tropics where the evergreen habit is predominant. The relatively large size of nearly half of the Dakota leaves is another point of resemblance to living foliage of low latitudes. The percentage of Dakota leaves with palmate (or plinerved) venation does not offer conclusive evidence. Far more significant would be figures on the relative number of camptodrome and craspedodrome leaves, but since this feature has not been considered in previous leaf

[5] Lesquereux expressed uncertainty regarding the generic status of some of his leaves by referring them to such form genera as *Protophyllum, Proteoides,* and *Phyllites.* And at one point (1891: 231) he asked the question. "Is *Sassafras (Araliopsis) platanoides* referable to *Sassafras,* to *Aralia,* or to *Platanus?*"

TABLE I. *Leaf characters of dicotyledons, showing percentages in each category*

Flora	Margin		Length		Venation		Texture	
	Entire	Non-entire	Over 10 cm.	Under 10 cm.	Pal-mate	Pin-nate	Thick	Thin
Dakota, 200 species.	73	27	44	56	27	73	74	16*
Lance, 46 species....	54	46	41	59	46	54	67	33
Medicine Bow, 42 species.....	67	33	45	55	40	60	71	29
Laramie, 55 species..	71	29	45	55	36	64	73	27
Panama, 41 species (modern).....	88	12	56	44	17	83	98	2
Bridge Creek, 20 species	15	85	30	70	30	70	55	45
Muir Woods, 22 species (modern).	23	77	27	73	23	77	64	36

*This number includes those designated as thin in Lesquereux's descriptions and also those whose texture was not noted and which may be presumed not to have been thick.

analyses, adequate comparisons cannot be made here. However, it should be noted that 72 per cent of the Dakota leaves have camptodrome nervation, which relates the flora to tropical rather than to temperate forests of today. Comparison with data assembled by Dorf (1942: 101, Table I) for later Cretaceous floras of the Rocky Mountain area indicates a striking similarity to their leaves and to those of a modern forest in Panama. There is a marked difference between the Dakota leaves and those of the middle Tertiary Bridge Creek flora and of the modern forest of Muir Woods. Dorf considers the Lance and Medicine Bow floras to indicate climatic conditions intermediate between warm temperate and subtropical, and the Laramie flora as definitely subtropical; the Bridge Creek and Muir Woods floras are temperate. On the basis of the characters of its angiosperm leaves, the Dakota flora may be supposed to have lived under conditions more subtropical than temperate. In apparent agreement with this assumption are several ferns and Cycadophytes which are suggestive of a frost-free climate. The sediments in which all these plants are preserved indicate a floodplain deposit.

In conclusion, we may consider the habitat relationship of *Pinus clementsii* to this lowland forest. Unlike many of the angiosperms, its generic status appears to be above question, and the only doubtful element of our appraisal is whether this pine occupied the same habitat as the majority of those now living. In support of our opinion that *Pinus clementsii* was an upland tree rather than a member of the valley forest, the scarcity of its needles is in marked contrast to the abundance of angiosperm leaves. Furthermore, the smoothed surfaces of all except one of the cones suggests transportation for some distance before their ultimate deposition on a floodplain; this would have involved floating rather than dragging along the bed of the stream, for the cones of living pines are buoyant for a week or more until they become water-soaked, and our specimens show no evidence of heavy abrasion. The Dakota sediments themselves are also indicative of adjacent high relief, for the sands are poorly assorted and cross-bedded, and layers of gravel or conglomerate with well-rounded pebbles may make up a conspicuous part of many sections exposed (Stauffer and Thiel 1941: 99-104, 128-130). The cones and leaf which are the subject of this paper appear to have been washed down from these not distant highlands into the valley occupied by the earliest known forest of Minnesota.

In Japanese art and literature the pine, matsu, is a symbol of strength and longevity. In their home on the mountains, we are told, pine trees reach a great age and hold their branches high against the wind. Such is the history of the red pine, whose ancestry extends back for a hundred million years, through intervals of climatic vicissitude, to the Clements pine of the Cretaceous.

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HISTORY AND EVALUATION OF VARIOUS CONCEPTS OF PLANT AND ANIMAL COMMUNITIES IN NORTH AMERICA[1]

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Introduction

A community is a unit aggregation of organisms made up of a distinct combination of species. That certain species are ordinarily found together and are characteristic of certain habitats has doubtless been common knowledge since intelligent man first evolved. In the fourth century, B.C., Theophrastus, a friend of Aristotle, recognized that associated plant species may interact among themselves and with their environment. As a consequence he has sometimes been considered the first ecologist (Ramaley 1940). Grisebach, however, has been credited (Gleason 1939) for having presented in 1838 the first modern discussion of the integrated nature of plant communities. Mobius' account of an oyster biocoenose in 1877 is one of the first descriptions of an integrated animal community. Forbes showed in 1887 how plants and animals living together in lakes form a self-sufficient microcosm. That plants and animals are essential interacting elements in all communities led to the development of the biome concept in the present century by Frederic E. Clements and Victor E. Shelford. It is the purpose of this paper to trace the historical development and application of this concept and to evaluate it in relation to other methods of analyzing plant and animal distribution.

I wish to acknowledge at this point the helpful suggestions of my colleagues who read parts or all of the manuscript in its preliminary form, especially Dr. Hobart M. Smith, herpetologist; Dr. D. F. Hoffmeister, mammalogist; Dr. Harvey I. Fisher, ornithologist; and Dr. A. G. Vestal, plant ecologist.

History of Biogeography of North America

Early explorations

Harshberger (1911) has listed the early botanical explorations of North America and Engler (1899) also has a detailed review of the development of plant geography during the nineteenth century. It is sufficient for background here to mention only a few of the more important explorations. The first botanical accounts came from the Spanish explorations in the West Indies and Mexico, beginning in 1535. Mark Catesby published on the natural history of Carolina and Florida (1731-43). The first collections of plants and animals on the Pacific coast were made during the last quarter of the 18th century by scientists accompanying the French, Dutch, English, and Spanish boats that stopped at various points all the way from Tierra del Fuego to Bering Strait.

It was not until the early part of the 19th century that explorations into the interior of North America yielded much of interest. The Lewis and Clark expedition came in 1804. Zebulon Pike began his explorations in 1805. Thomas Nuttall traveled extensively over the interior between 1809 and 1834. Reports of plants collected by Stephen H. Long's party were published in 1822 and 1824. John C. Frémont explored from the central Rockies to the Pacific coast between 1842 and 1848. John Torrey's report on the botany of the United States and Mexican Boundary Survey came in 1858. Extensive publications on both plants and animals resulted from the surveys conducted to ascertain the most economical route for a railroad from the Mississippi River to the Pacific Ocean between 1855 and 1861. G. M. Dawson and John Macoun explored western Canada between 1872 and 1881, and Rothrock had a flora of Alaska in 1867. These extensive surveys and many others laid the foundation for the recognition of major community units on the continent and an increased refinement of biogeographical analyses as time went on.

Origin of biogeography

Zoogeography may be said to have originated with the extensive writings of the illustrious French naturalist, Georges L. L. Buffon, who lived from 1707 to 1788. According to Gill (1885: 1-2), Buffon recognized : (1) that the inhabitants of the tropical and southern portions of the old and new worlds were entirely different from each other; (2) that those of the northern portions of the two were, to a considerable extent, identical; and (3) that the confluence of the two was most apparent towards the proximate portions of America and Asia. The truth that animals in fact had, for the most part, originated in the regions of the

[1] This paper is a condensation of a presidential address delivered before the Ecological Society of America at Ithaca, N. Y., in September, 1952.

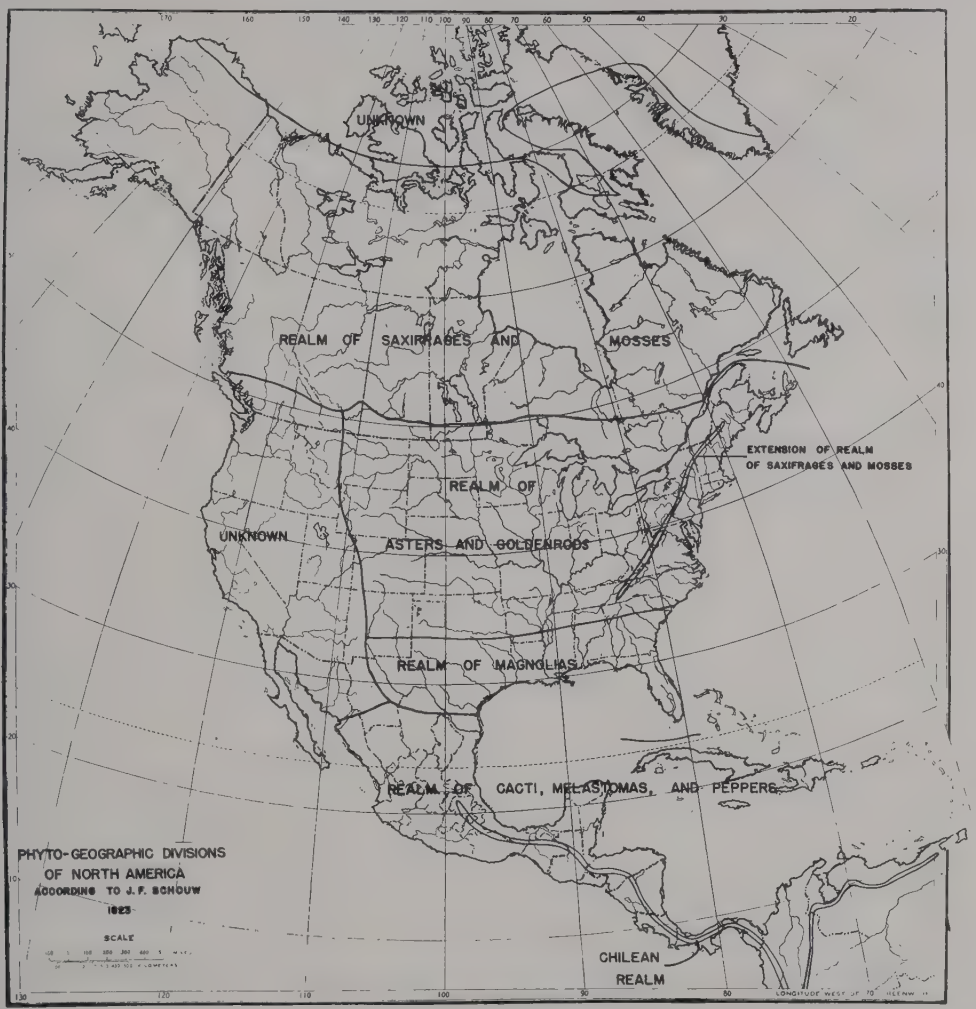

FIG. 1

earth where they are now found, became incontrovertible; and geological research demonstrated that they were preceded by forms which were the ancestors of those now living on the soil.

The beginnings of phytogeography as a distinct science may be associated with the writings of Alexander von Humboldt whose life span extended from 1769 to 1859. He traveled extensively over the world, recognizing and describing types of vegetation, and correlating plant distribution with climate (1807, 1820). He placed emphasis on the general appearance and physiognomy of the predominant mass of the vegetation for characterizing his various vegetation types.

It will be profitable now to trace briefly in chronological order the major contributions to the biogeography of North America.

Joakim Frederik Schouw (1823, Fig. 1).— The earliest map of North America that has come to my attention, that shows either plant or animal subdivisions, is the one prepared by Schouw, a student of Humboldt's. Each division was called a "Reiche" or realm and was based on a statistical analysis of plant distribution which required one-half of the known species, one-fourth of the known genera, and at least some families to be restricted to or to reach their maximum development in the area.

C. Pickering (1830).—C. Pickering, M.D., divided North America into the following large botanical regions:

I. Greenland, Iceland, and arctic regions which extend over both continents. Arctic plants also extend an indefinite distance southward in the Appalachian and Rocky Mountain Systems. The Cascade-Sierra Nevada System is, however, not shown on his map.

II. Temperate portion of North America. This region was in turn subdivided into sub-regions.

1. Flora Canadensis—all Canada, from the Atlantic to the Pacific, and bounded south by the Columbia, Missouri, and St. Lawrence rivers.

2. Flora of the United States—the country situated between the Atlantic Ocean and the Mississippi River.

3. Flora Ludoviciana—the country between the Mississippi River and the northern Andes (Rocky Mountains).

4. Flora Californiana—the country between the northern Andes and the Pacific.

III. West Indies and the intertropical region of America.

His recognition of three great north and south divisions across the middle of the continent (II, 2, 3, 4) represents a concept that was to receive considerable attention for many years to come, although the concepts of the boundaries between the three regions were to vary considerably.

F. J. F. Meyen (1836).—Meyen was Professor of Botany at the University of Berlin. His ideas were much influenced by von Humboldt's emphasis on general physiognomy of landscapes and types of vegetation and he criticized Schouw's "statistical classification of vegetation." He first divided the world horizontally into eight zones bounded by particular degrees of latitude and degrees of temperature and each characterized by particular physiognomies and kinds of plants. He next divided the vegetation vertically into regions of palms and bananas, tree ferns and figs, myrtles and laurels, dicotyledonous trees, Abietinae, rhododendrons, and alpine plants.

A. Wagner (1846-1851).—Wagner was impressed with Schouw's plant geography and attempted to divide the world into animal provinces based on the distribution of mammalian species. He recognized three broad zones each divided into provinces. The northern zone included the polar province, the temperate province of the Old World, and the temperate province of North America. The middle zone was divided into a South Asian province, an African province, and a middle tropical American province. The southern zone contained the Australian province and the Magellanian (southern South American) province. Wagner tried to correlate the distribution of animal groups with types of vegetation and races of man. The northern zone agreed more or less with the distribution of spruces. The polar province had many circumpolar species and was a region of lichens and mosses. The southern limit of the temperate North American province coincided with the limits in the distribution of firs.

Louis Agassiz (1845, 1854, Fig. 2).—Agassiz divided the world into Arctic, temperate, and tropical zones with the temperate zone further divided into sub-arctic, cold temperate, warm temperate, and sub-tropical zones. The temperate zone was limited by the isotherms of 32° and 74° F. He was impressed by the uniform distribution of animals in the Arctic zone continuous around the world but the temperate zone he divided into Asiatic, European, and American realms "in accordance with the prevailing physical features." South America was included in the American realm, even though it is tropical, because its animal life is more closely related to that of North America than to those of other tropical areas. The division of the American realm into faunas is "intimately connected with the conditions of temperature, soil, and vegetation." Agassiz's ideas and his mapping of major communities had considerable influence on later workers.

Amos Binney (1851).—Binney was first a physician, later a businessman, but with a hobby of studying land snails that he maintained throughout life. He divided temperate North America into: (1) an Atlantic region, extending from the Atlantic Ocean to the Appalachian Mountains; (2) a central region, from the Appalachian to the Rocky Mountains; and (3) a Pacific region, from the Rocky Mountains to the Pacific Ocean. He was impressed with the importance of mountains as natural barriers to animal dispersal and recognized that changes in vegetation had importance in controlling distribution of mollusks. On the basis of topography, climate, and groupings of species of snails he divided the eastern part of the country into "sections": I. Florida, II. the region with extensive forests of pine corresponding more or less to the Louisianian or Austroriparian faunal area of later workers, III. a region about equivalent to that covered by the mixed mesophytic forest, IV. a northern interior district which with III would coincide roughly with the Carolinian faunal area in the later life-zone system, and V. and VI. which together agree more or less with the Alleghanian faunal area.

John L. Le Conte (1859, Fig. 3).—Basing his conclusions upon the study of the geographical distribution of coleopterous insects (p. iii), ". . . the whole region of the United States is divided by meridional, or nearly meridional lines into three, or perhaps four, great zoological districts,

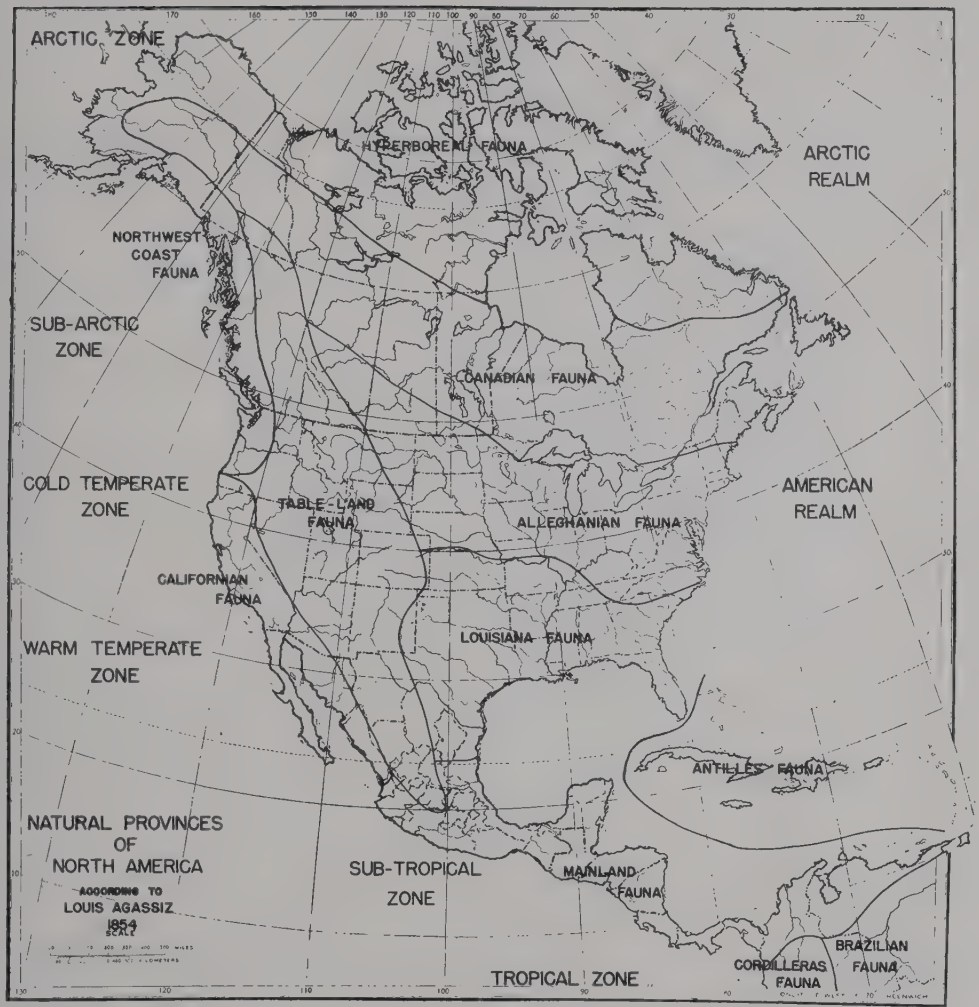

FIG. 2

distinguished each by numerous peculiar genera and species, which, with but few exceptions, do not extend into the contiguous districts." The eastern district extended from the Atlantic Ocean to the beginning of the arid prairies and included the entire coastal region of Texas, the central district extended from here to the Sierra Nevada of California, and the western district was the western slope of the mountains in California, Oregon, and Washington. The major districts of Le Conte are further divided ". . . into a number of provinces, of unequal size, and which are limited by changes in climate." The subdivisions of the Atlantic district into northern, western and middle, and southern provinces; of the central district into northern, middle eastern, and southeastern provinces; and of the Pacific district into northern, Californian, and southern provinces represents a partial lay-out of the scheme later to be known as the life-zone system.

J. G. Cooper (1859, Fig. 4).—J. G. Cooper, M.D., divided the country into "natural provinces" and into subdivisions, "regions." He gave each province and region a name, often a geographic name, frequently an Indian name. Many of these names are being used, even at the present time, for *biotic provinces* (Dice 1943), and in fact there is some agreement between the boundaries

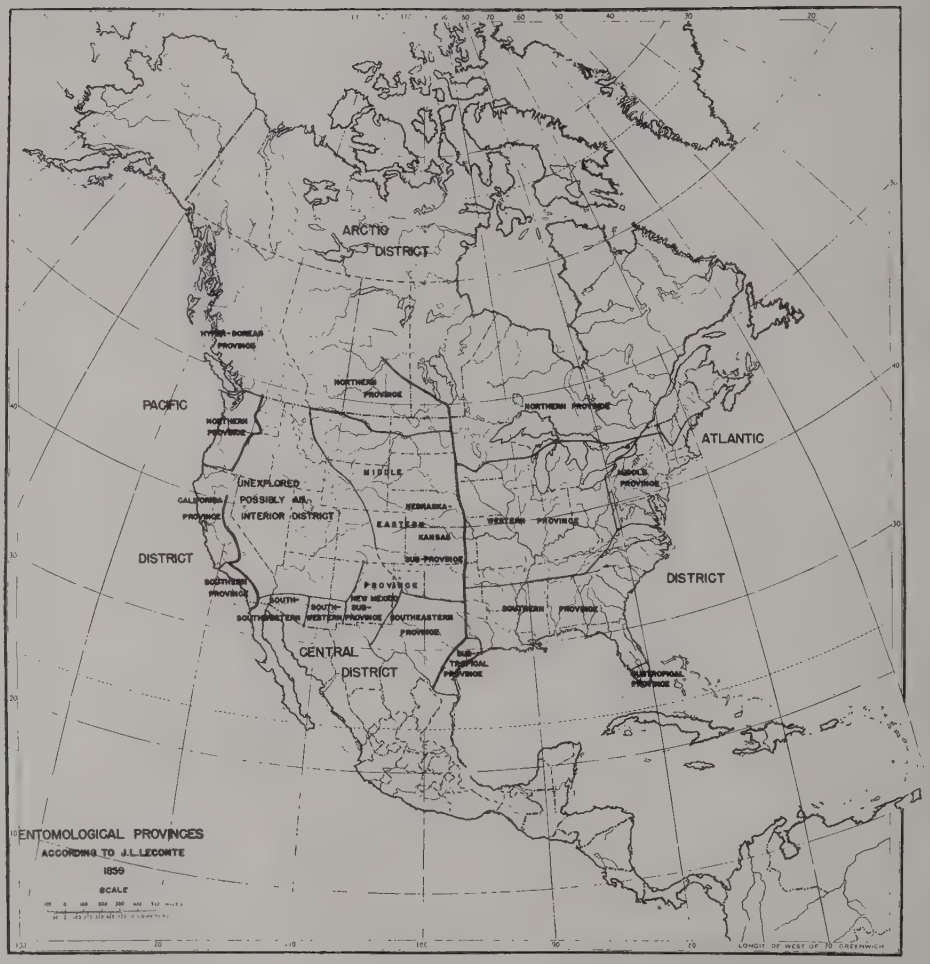

FIG. 3

of some biotic provinces and certain of the *regions* first defined by Cooper.

Cooper's *provinces* are based largely on differences in type of vegetation. In this respect they anticipate the *biome* concept of modern time. This correlation is even more significant since Cooper was fully aware that several of the provinces were characterized by distinctive animals as well as plants, although he does not list the animals specifically.

The distinction between *regions* is based largely on the differences between species to be found in the areas and also on less conspicuous differences in vegetation-type. The exact boundary lines of regions were drawn as far as possible in harmony with isotherms, physiographic features, elevation contours, and changes in vegetation.

It appears that Cooper's understanding of plant and animal distribution was ahead of his time. Actually, he was more nearly bioecological in his thinking than many who were to follow during the next half-century.

Edward D. Cope (1875).—Cope worked principally with amphibians and reptiles but gave lists of species in all vertebrate groups that characterized the six regions of North America which he recognized but did not map: Austroriparian, including Floridan, Louisianian, and Texan dis-

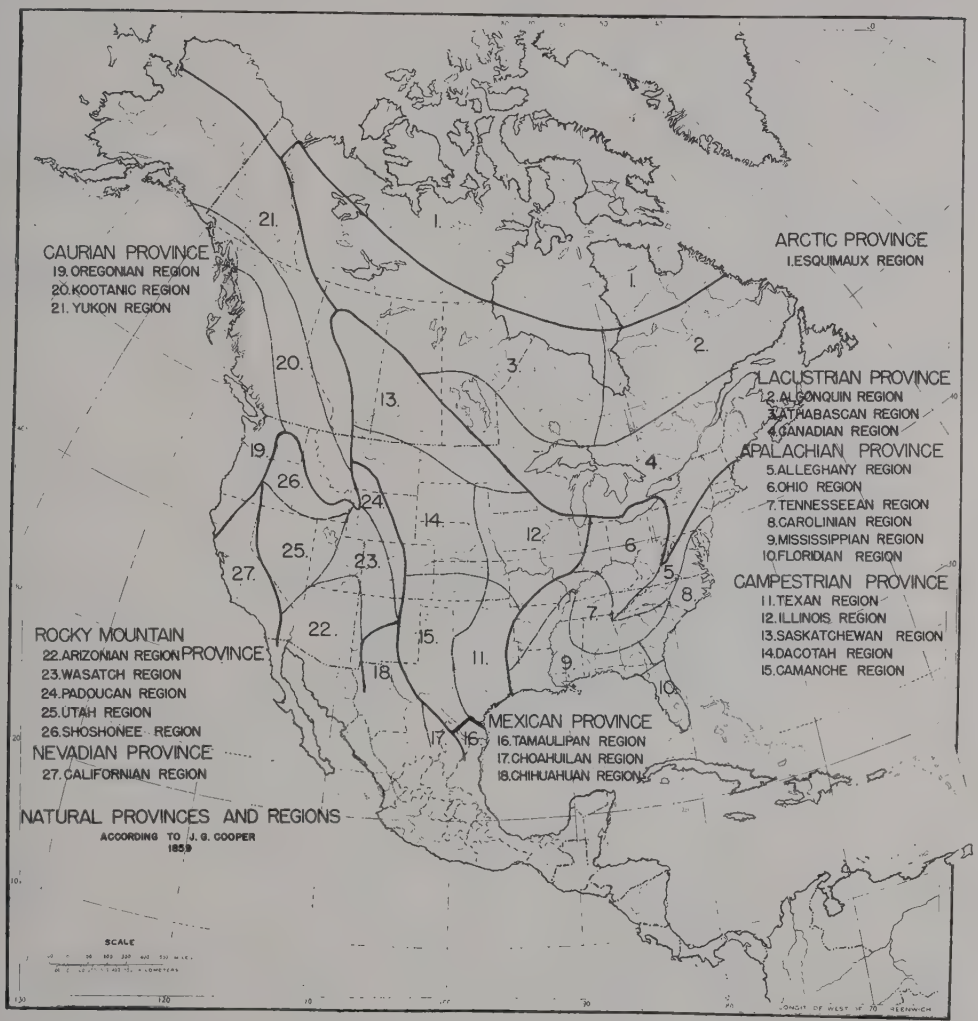

FIG. 4

tricts; Eastern including Carolinian, Alleghanian, Canadian, and Hudsonian districts; Central, which was divided into a Plains district (grassy) and a Rocky Mountain district (sagebrush); Pacific, west of the Sierra Nevada; Sonoran in the southwest; and Lower Californian. Cope was the first to define these latter two regions. The Sonoran region included parts of eastern California, Nevada, New Mexico, Arizona, and Texas and extended south into western Mexico. The further development of a life-zone terminology at this time is of interest.

August Grisebach (1872).—Humboldt's emphasis on the interpretation of vegetation from the point-of-view of its physiognomy and its correlation with climate had considerable influence on Grisebach who developed the philosophy in considerable more detail. As early as 1838, Grisebach had applied the term "formation" to vegetation of uniform physiognomy (Clements 1916: 116). The extensive regions that he recognized in North America depended on the similarity in vegetative form of the conspicuous predominant plants. Each region contained one or more formations depending on differences in the climate and on differences in the evolutionary and geological history of the vegetation and region. We begin to see here the impact of Darwin's evolutionary concepts on the interpretation of vegetation.

Grisebach's Arctic flora included tundra and alpine vegetation. The forest region of the Western Continent he treated as a single formation but in describing it, broke it down into "zones" more or less equivalent to what we now know as boreal forest, montane and coast forest, pine-hemlock-northern hardwoods, deciduous forest, and broad-leaved evergreens and southern pines. The prairie region was subdivided into an eastern prairie or grass steppe formation, a western salt steppe formation, and a southern scrub formation. The California coast region was a park formation made up of conifers, broad-leaved trees, evergreen shrubs, and grass. The Mexican region contained many varied vegetation forms and the beginning of the tropical forest and savanna.

Adolph Engler (1882).—The German botanist, Adolf Engler, published extensively on the phytogeography of the world and in 1882 presented a classification, showing a hierarchy of taxonomic or floral units.

The extratropical realm in North America included Arctic, Atlantic, and Pacific regions and the neotropical realm included the Mexican highlands and tropic regions. These regions, in turn, were subdivided into provinces, and some of the provinces were further divided into zones and then into districts. Regions were correlated with differences in climate, provinces with physiognomy of the plants, while zones and districts depended largely on the geography of smaller taxonomic units.

FIG. 5

In addition, he also mapped types of vegetation which were based largely on the life form of the conspicuous predominant plants. A close study of his maps, which are not reproduced here, shows a confusing lack of agrement between his floristic and vegetative divisions.

Oscar Drude (1884, 1887, 1890, Fig. 5).—This German professor of botany and director of the Royal Gardens at Dresden was much influenced in his thinking by the writings of August Grisebach. The basic fundamentals of plant geography he believed to be three: (1) plants are affected in their occurrence and development by climatic conditions; (2) plant distribution is dependent upon such geological factors as barriers, size of land areas, and the relation of land masses to each other; and (3) the general characteristics of vegetation are best shown by its physiognomy. He presented three sets of maps to show separately the way each of these fundamental concepts may be applied. Perhaps Drude's most interesting ecological contribution is his mapping and description of vegetation regions or "formations." This analysis is more detailed and accurate than that of either Engler of Grisebach, and we note the recognition of the more important types of vegetation that appear on all maps of the present day.

Joel Asaph Allen (1871, 1878, 1892, 1893, Fig. 6).—J. A. Allen differed vigorously from Sclater (1858) and Wallace (1876) in the manner in

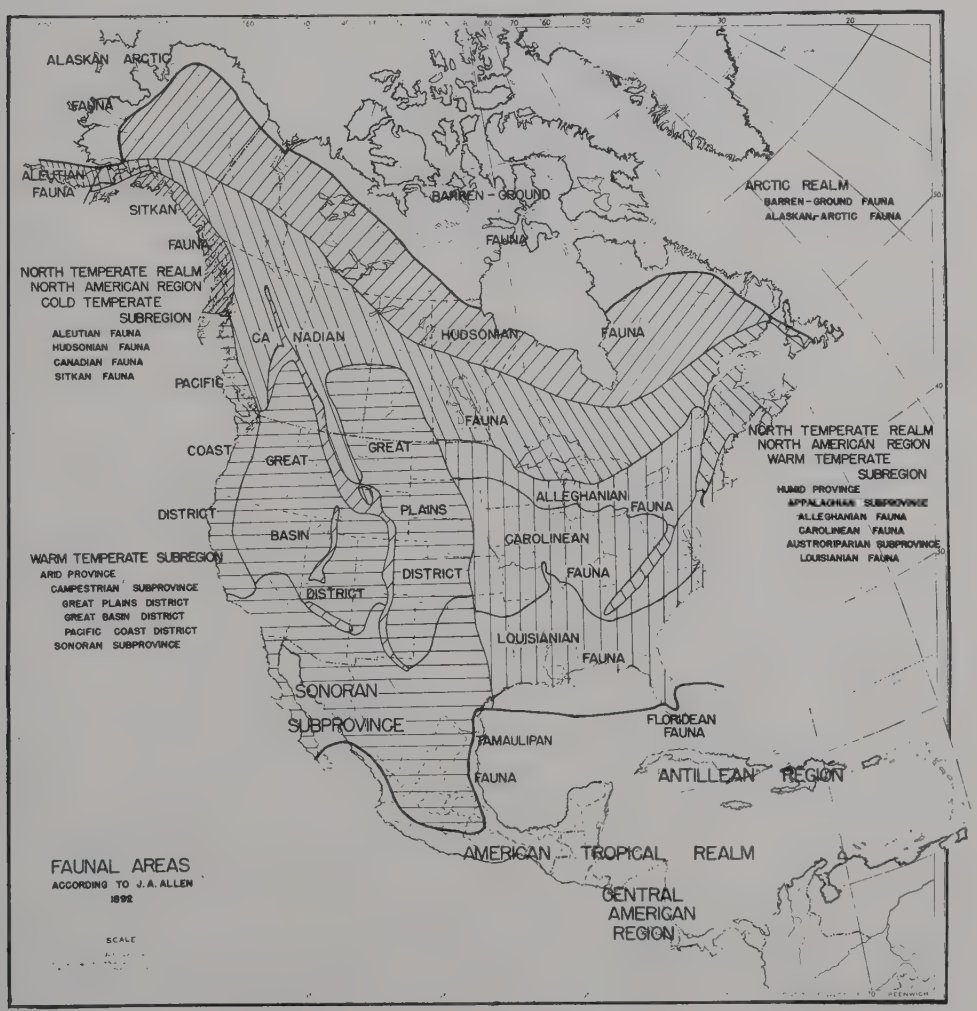

FIG. 6

which the world should be divided into major communities. He recognized arctic and north temperate realms that were circumpolar and a separate American tropical realm. The north temperate realm he divided into North American and Europaeo-Asiatic regions and into cold temperate and warm temperate subregions. Subregions were in turn subdivided into provinces and districts largely because of the important effect of humidity in controlling forest distribution and the animal life associated with forests.

The reason that the dividing line between the eastern humid and western arid provinces was made at the 100° meridian, at the edge of the Great Plains, rather than at the junction of the eastern forests with prairie is given in the following statement (1871: 387-388): "At the junction of the prairies with the eastern wooded districts there is quite an appreciable change in the fauna, especially in respect to the birds and mammals. The faunal differences between these regions, in respect to these two classes, result mainly through the addition of a relatively smaller number of strictly prairie species, the western extension of none of the species of the Eastern Province wholly terminating at this point. The number of their representatives, however, becomes greatly reduced, and their distribution from being general and uniform is restricted to the belts of forest skirting the streams. At the eastern limit of the prairies, in fact, the distinctly western species begin to appear, thence westward few additional western species being met with till the edge of the great central plateau of the continent is reached, where the differentiation is further increased not only by the addition of many new forms, but by the gradual disappearance of eastern types. Whether the addition of a few prairie species be sufficient reason for recognizing a western subdivision of each of the faunae of the Eastern Province may perhaps be thought questionable."

In this hierarchy of terms and areas developed by Allen, realms are sometimes characterized by orders of animals, commonly by families; regions usually by genera and sometimes by families; provinces ". . . by the presence or absence of prominent generic types"; and faunas ". . . not . . . by the presence or absence of particular genera or species but by the association, through the overlapping of their habitats, of a number of genera and species not elsewhere found together. . . ." (1892: 204).

C. Hart Merriam (1890, 1891, 1892, 1898, 1910, Fig. 7).—In 1889, Merriam and his assistant, Vernon Bailey, in the Division of Ornithology and Mammalogy, were granted $600 by the U. S. Secretary of Agriculture and two months time to undertake a survey of the San Francisco Mountains in Arizona. The most important conclusions arrived at in this study, which included both plant and animal life, may be given in Merriam's own words (1890: 1-2): "(1) The discovery that there are but two primary life areas in North America, a northern (boreal) and a southern (subtropical or Sonoran), both extending completely across the continent and sending off long interpenetrating arms.

"(2) The consequent abandonment of the three life areas commonly accepted by naturalists, namely: the eastern, central, and western provinces.

"(3) The recognition of seven minor life zones in the San Francisco Mountain region, four of boreal origin (alpine, timberline, Hudsonian, Canadian), and three of subtropical or mixed origin (neutral or transition, piñon, desert).

"(4) The correlation of the four boreal zones with corresponding zones in the north and east."

After making a study in Idaho (1891) and an extensive and thorough review of literature, he was ready in 1892 to correlate the subtropical or Sonoran zones of the west with corresponding zones in the east. "It can now be asserted with some confidence not only that the transition zone of the west is the equivalent of the Alleghanian of the east but also that the upper Sonoran is equivalent of the Carolinian, and the lower Sonoran of the Austroriparian, and that each can be traced completely across the continent" (1892: 22). In 1898, Merriam adopted the terms transition, upper austral, and lower austral for these three zones and these names have persisted to the present day. Influenced doubtlessly by Allen and earlier workers, Merriam (1892) divided these three zones into humid eastern and arid western divisions along approximately the 100° meridian, but these were secondary divisions, not primary ones as Allen maintained.

Merriam's life-zone system was generally accepted with enthusiasm by mammalogists and ornithologists but less extensively by other zoologists and botanists. Perhaps part of this enthusiasm was due to the fact that the various units used were not just convenient geographic pigeon-holes for segregating distributional data but were challenging for the analysis of faunas in terms of origin, dispersal, and evolution, which previous systems had not emphasized. The publication of Darwin's theory of evolution in 1859 and the evolutionary point of view of Wallace doubtlessly had a considerable influence on later geographical studies but time was required for this viewpoint to develop. We see it in the interpretations of floristics and vegetation made by the three Ger-

FIG. 7

man botanists, Grisebach, Engler, and Drude in the 1880's, but Merriam's is the first serious application of it on a detailed continental basis in North American zoogeography.

A. F. W. Schimper (1903).—This professor at the University of Bonn in Germany followed the viewpoint of von Humboldt and Grisebach in being concerned not with the floristic composition of various parts of the world but with the physiological adjustments of plants and the vegetation as a whole to environmental factors, particularly temperature, precipitation, and soil. He divided the distribution of plants into tropical, temperate, and arctic zones extending around the world. Because of variation in other climatic factors, particularly rainfall, these zones were further divided into districts, each characterized by the presence of particular formations. There were also many local or edaphic formations of restricted extent interspersed within or between the climatic or district formations. The formations recognized for North American were: tundra, summer-forest (including into a single unit, as did Grisebach, all of the northern and western coniferous forests and the deciduous forest), temperate rain-forest (broad-leaved evergreen forest of the southeast), grassland, park-like savannah (mixed forest and meadow), desert, sclerophyllous woodland (Cali-

fornia), tropical xerophyllous woodland (savannah and thorn forest), luxuriant tropical rain forest, and monsoon forest. On the whole, it seems that Schimper's interpretation of the formation is a very broad and generalized one and the map of North America that he published is much less detailed and useful than are some earlier ones.

John A. Harshberger (1911).—The chronological history of attempts at mapping plant and animal communities in North America may be brought to a close with the contribution of John A. Harshberger, then Assistant Professor of Botany at the University of Pennsylvania. It seems unnecessary to give any special discussion of the work of Rikli (1913), Hayek (1926), and others.

Although Harshberger had a detailed knowledge of the present vegetation, had summarized data concerning the evolution and dispersal of floras since Cretaceous time, and had studied the immediate effects of the last retreat of the Pleistocene glacier, it is interesting that his floristic system of classification is reminiscent of the various attempts of the latter half of the nineteenth century, even to the extent of still dividing the temperate zone into Atlantic, interior, and Pacific sections. The sections are further divided in considerable detail into regions, districts, and areas. His interior section begins, however, at the eastern edge of the prairies, rather than at the beginning of the Great Plains as it did in many of the earlier maps, and extends to the Sierra Nevada and Cascade Mountains. It includes such diverse vegetation types as the prairie, Rocky Mountain coniferous forest, and Great Basin desert. His map is published in a variety of color, however, and he has distinguished tundra, forest, prairie, desert, and tropical types of vegetation regardless of the floral subdivisions in which they occur.

Summary.—Zoogeography and phytogeography may be considered as becoming distinct branches of science in the latter part of the eighteenth century with the work of Buffon and von Humboldt. Development of research and analysis during the nineteenth century went along four principal lines; floristics, vegetation, faunistics, and biotic. Additional workers than those specifically mentioned in the above account participated in the development of these points of view although perhaps in a less important manner.

In floristics and faunistics, emphasis was placed on the quantitative composition, distribution, and geological history of taxonomic groups in geographic areas regardless of their segregation, relative abundance, or importance in different habitats or ecological communities within the areas. Schouw, Pickering, Candolle (1855), Gray (1856-57, 1880), and Sargent (1884) restricted themselves largely to floristics, while most zoologists were concerned only with faunistics (Agassiz, Amos Binney, Woodward 1856, Le Conte, Baird 1866, Murray 1866, W. G. Binney 1873, Cope, Wallace 1876, Packard 1883, Heilprin 1887). The development of the evolutionary theory with the work of Darwin and Wallace had a profound effect upon this aspect of plant and animal geography. There can be no question that the development of the historical and phylogenetic aspects is a very important contribution to ecological philosophy.

When we speak of "vegetation" we refer to the total plant population viewed from the anatomical and physiological rather than from the taxonomic viewpoint. Vegetation units such as prairie, desert, deciduous forest, etc. are characterized chiefly by the physiognomy of the conspicuous dominant species. Investigators who were primarily concerned with the analysis of vegetation were von Humboldt, Meyen, Grisebach, and Schimper. There is considerable difficulty, however, in completely divorcing the analysis of vegetation from that of the flora. Engler, Drude, and Harshberger considered both points of view and made some attempt to combine them.

Some of the early geographers pointed out agreements between the distribution of plants and animals or between animals and types of vegetation. The aim was primarily to use the same geographic units for both the flora and the fauna rather than to depict any fundamental interdependence between the two. This procedure is evident in the work of Berghaus (1838), Wagner, Schmarda (1853), Allen, and Merriam. Usually the primary emphasis was either on plants or on animals and correlations between the two were largely incidental. Some of the faunistic geographers however, acknowledged the importance of humidity or precipitation in controlling animal distribution by determining the prevalent type of vegetation and niches for animals. It would seem that Cooper, especially, came close to a truly biotic point of view that anticipated to some extent its present day emphasis.

Modern Concepts of Communities

Floristics

Recent studies, such as those of Good (1947), Camp (1947), Raup (1947), and others are concerned more with analyzing and interpreting the distribution of taxonomic units from the viewpoint of geological origin, dispersal pathways, phylogenetic relations and evolution, and control by climate, soil, topography, and continental configu-

rations than they are in setting up community units. Such units as they define are primarily for convenience in pigeon-holing the distributional data that they acquire rather than as serving a primary basis for further analysis.

Cain (1947) emphasizes the need for purely objective procedures in mapping floristic regions. The distributional limits of each species should be drawn by a line around the peripheral spots of occurrence known from actual specimens collected. Superimposition of outline maps of all species should suggest natural boundary lines between regions without the doubtful subjective procedure of selecting representative species. The difficulty with this method is that the distribution of many species is poorly known, and floristic regions determined for one taxonomic group may not be suitable for other groups.

A somewhat different procedure is the analysis of a local flora into endemic and extraneous elements. Cain (1947) states that "floral elements" should be defined in relation to their probable origin locally or to some center lying outside the region under study. Floral elements are not geographic units but rather groups of species having a common history. It would seem possible that eventually a list of the major floral elements of the continent could be compiled.

Vegetation

In the study of vegetation, instead of individual taxonomic units being emphasized, it is the kind of aggregation that they form that is of major consideration. Shreve (1917) and Livingston and Shreve (1921) were concerned with "the growth forms involved, the presence of one or many strata of plants, the open or closed condition, and the degree of simplicity or complexity of the specific content." Secondary criteria employed in the classification of vegetation were "the physical nature of the habitat and the specific identity of the plants concerned. . . ." Some 18 different types of vegetation were recognized.

Shantz and Zon's (1924) map of vegetation of the United States has been much used. The major units of vegetation recognized in the United States are forest vegetation (eastern and western), grass, and desert shrub. The forest vegetation is subdivided geographically and taxonomically on the basis of the principal genera and species of trees involved; grassland is subdivided largely on the life-form of the grasses, general physiognomy, and secondarily by its species composition; and desert shrub primarily by the principal species involved which, however, correspond in a general way to a physiognomic classification. It is obvious, therefore, that Shantz and Zon's classification is not entirely a vegetational one. However, the lapse over into floristics in the secondary divisions is due to lack of proper procedures for describing local or even regional variations in the same general type of vegetation.

Further advancement of the vegetational approach to the distributional study of plants obviously requires more refined methods for defining and describing the vegetation other than by floristics. Raunkiaer's (1934) system analyzes the proportions of different life forms in the total flora of a region but fails to evaluate different species on the basis of their abundance and relative importance in the community. Recent schemes proposed by Küchler (1947) and Dansereau (1951), however, seem to have considerable promise and should be given thorough testing. A simple workable method of describing vegetation would be of great value to animal ecologists.

Faunistics

The point-of-view in faunistics is very similar to that of floristics and studies are largely undertaken by taxonomists. Recent attempts at a zoogeographic classification of the world are those of Metcalf (1933, 1946) and Beaufort (1951). For further analysis of the faunistic point of view, separate consideration needs to be given to life-zones, biotic provinces, and faunal groups.

Life-zones.—The latest contribution of Merriam to the concept of life-zones was a detailed map prepared by himself, Bailey, Nelson, and Preble in 1910. This is the map that is commonly reproduced in present-day books. A very recent life-zone map has been published by Muesebeck and Krombein (1952). The only significant revisions seem to be in Alaska where more arctic zone is indicated and in the southern tip of Texas where a small area of tropical zone is shown. The map facilitates the author's indication of distributional ranges in their synoptic catalog of North American Hymenoptera.

An essential part of the life-zone concept as developed by Merriam is belief in the preponderant role of temperature in controlling distribution. In 1894 he proposed two temperature laws, one to control the northward dispersal of organisms, the other to control their southward dispersal, but these laws have since been found faulty (Kendeigh 1932, Shelford 1932, Daubenmire 1938, 1946). Insofar as the boundaries of life zones are not defined biotically but are made to agree with isotherms (*e.g.*, Klugh and McDougall 1924), they are highly questionable.

Probably the biggest mistake that Merriam made was in making transcontinental belts of his zones (Dice 1923, Daubenmire 1938, Miller 1951), but this followed naturally after adoption of temperature as the primary controlling environ-

mental factor. It appears that most modern day adherents and users of life-zones apply them only locally or regionally and mostly disregard or ignore the transcontinental implications involved.

H. M. Hall and Grinnell (1919) defined life-zones, as they occurred in the western mountains, as "primarily biologic, that is, they are composed of and determined by a certain assemblage of plant and animal species." Because the life-zones were not everywhere continuous and were influenced considerably by changes in local habitats, the authors selected sets of indicators that would identify the biological area wherever found. These indicators consisted of both plants and vertebrate animals exclusive of fish. E. R. Hall (1946) similarly used types of vegetation for identifying life-zones in his study of mammal distribution in Nevada. This procedure seems to be modifying life-zones into bio-ecological, rather than strictly faunistic units.

Miller (1951: 617) found plant communities and physical habitats more precise than life-zones for analyzing bird distribution in California because they are more finely differentiated (21 units compared with 4 or at the most 6) and because the distribution of the community units reflected the influence of all climatic or environmental factors rather than temperature alone. Of the 260 species analyzed, only 54 species were confined to a single life-zone, the majority ranged over two or three zones, and a very few occurred in four or more zones (Kendeigh 1952).

In general it appears that while life-zones have proved useful in the past, especially in mountainous terrain, other systems for analyzing animal distribution have been developed in recent years that serve the same purpose more effectively and are more detailed and exact.

Biotic provinces.—The term and concept of "biotic province" was used regularly in the classroom instruction of H. A. Gleason at the University of Illinois and appeared in publications of his students, Gates in 1911 and Vestal in 1914. A biotic province, as defined and mapped by Dice (1943: 3), is a "considerable and continuous geographic area . . . characterized by the occurrence of one or more important ecologic associations that differ, at least in proportional area covered, from the associations of adjacent provinces. In general . . . characterized also by peculiarities of vegetation type, ecological climax, flora, fauna, climate, physiography, and soil." Dice states further (p. 6) that ". . . the limits of geographic range of species and races of plants and animals are not fully satisfactory criteria for determining the boundaries of biotic provinces and districts."

Several types of vegetation and ecological climaxes may occur in the same province. The Navahonian province, for instance, includes alpine meadow, subalpine forest, montane forest, chaparral, piñon-juniper woodland, and arid grassland "life belts." The primary requirements of a province is to be a continuous geographic unit which has a combination of characteristics not found in adjacent provinces. Provinces, hence, never occur in discontinuous fragments, and they seldom include the whole of any vegetation type. It seems that in actual practice the boundaries of provinces are determined by the ranges of at least key species or subspecies.

Goldman and Moore (1946: 347-348) state that biotic provinces " . . . are regional areas embracing natural general groupings as shown by the analysis of species and considerations that may include biotic relationships and geologic history." These authors state further that biotic provinces ". . . . are designed to present a nearly balanced concept of the major centers of distribution in the country as a whole." This concept is further supported by Smith (1949: 229) who defines biotic provinces as ". . . continuous geographic areas possessing a fauna distinguishable to a certain degree from those of all adjacent areas." In further explanation he states (p. 225) that ". . . . they are sufficiently distinct that wide ranging species can, more often than not, be expected to possess variations closely correlated geographically with the general limits of the provinces. . . . the difference(s) may be either lesser or greater than subspecific rank." In order to facilitate agreement in demarking biotic provinces he recommends (p. 227) ". . . a separate index for establishment of biotic areas by percentage distinctiveness of each of the herpesian, avian, and mammalian faunae." He believes (Sanders and Smith 1951) that most schemes of provinces that have been worked out are not truly "biotic" but are actually in practice based upon the distribution of restricted groups of animals. Webb (1950) limited biogeographical areas in Texas and Oklahoma to areas with at least 75 per cent similarity of species between stations 100 miles apart.

In contrast to life-zones which attempt to make broad horizontal correlations of animal and plant life across the continent on the basis of agreement in genera present, the biotic province is intended to show regional areas of differentiation, especially at the level of species and subspecies. A mountain range may have several life-zones represented on it but only a single biotic province, provided there is a similar tendency for specific or subspecific distinctiveness of the fauna in all the zones. The two concepts, therefore, have quite different objectives.

Faunal groups.—Recently, faunas or faunal groups have been defined as ". . . associations of species with similar, though not identical, climatic and biotic tolerances, with ranges partly in common, and often with similar areas of origin as species" (Johnson, Bryant, and Miller 1948: 237). As such, faunas are not primarily geographic units but rather groups of species with common characteristics and history, similar in nature to the "floral elements" of some phytogeographers. Pioneer contributions to this change of emphasis in zoogeography are the analyses of continental origins of American herpetofauna by Dunn (1931) and avifauna by Mayr (1946).

Faunas, so defined, are not necessarily limited to any one type of vegetation, life-zone, or biotic province. Two or more different faunas may interdigitate or mix together in the same geographic area. A complete enumeration of discrete regional faunas of North America has not been made, but in describing the bird composition of California, Miller (1951) recognizes boreal, Great Basin, Sonoran, and Californian faunas and characterizes the various parts of the state according to the prevalence of the particular faunas present. This is an interesting and valuable method of analysis, but the distinguishing and description of faunas require considerable knowledge about past origins and histories of the component species involved, and this information may not always be available.

Plant associations and formations

According to a definition adopted by the International Botanical Congress of 1910 in Brussels (Wildeman 1910: 152) an "association" is a plant community of certain floristic composition, of uniform habitat conditions, and of uniform physiognomy. Floristic composition includes not only the list of species but also a sociological evaluation based on their abundance, dominance, sociability, constancy, fidelity, vitality, periodicity, and rhythm. It is assumed that a uniform floristic composition is an indicator and expression of a uniform habitat and that the prevailing physiognomy is an effect produced by the habitat on the plants, especially on the life-form of the dominants.

According to some European schemes, analogous associations combine to form "federations" or "alliances" and these group together into "subformations" or "orders" and finally the highest grouping of communities is into "formations" or "classes." Thus this concept starts from a floristic basis, although primarily concerned with the conspicuous, abundant, or dominant plants, and gradually works up to a vegetative basis in the higher categories (Braun-Blanquet 1932).

In his world map of vegetation, Rübel (1930, 1936) includes the following formations for the United States and Canada: polar and alpine treeless region, needle-leaved forest, summer green forest, hardgrass prairie, dry desert, sclerophyllous forest and scrub (California), and laurel-leaved forest.

The "cover type" of foresters is a forest type of distinctive character, considerable area, and "now occupying the ground, no implication being conveyed as to whether it is temporary or permanent." These cover types are named after one or two or sometimes three predominant species as judged by the "number of stems in the dominant and codominant classes combined." A committee in the Society of American Foresters recognizes 97 cover types in the eastern United States (Hawley 1932) and 50 in western North America (Baker 1945). In general, these cover types are based on finer distinctions than are the associations usually recognized by ecologists. Cover types often represent facies or faciations within the broader ecological unit.

Although it had been known in a general way for some time that one plant community may replace another as the habitat changed, the work of Cowles (1899) brought the concept vigorously to the attention of modern students. Clements (1916, 1920) and Weaver and Clements (1929) made major contributions to the advancement of ecology in North America by showing the successional relationships of communities to each other and by using these relationships as a basis for developing a classification of plant communities. Seral plant communities in the Clementsian scheme are called "associes" to distinguish them from climax communities which are "associations." The concept of association is more restricted in scope than that used by Europeans. Both the associes and association are recognized by the species composition of the dominant plants. Associations are grouped into "formations" when (1) the climax dominants belong to the same major life-forms, (2) when a large number of the dominant genera extend throughout the formation, though represented by different species in each association, and (3) when one or more dominant species occur in the various associations to at least some degree. Thus the formation of Clements is a tightly knit unit determined partly by the vegetation type and partly by floristics. Formations belonging to the same vegetation type are grouped into tundra, forest, grassland, woodland, scrub, and tropical climaxes.

Clements used the climax community as his fundamental unit of classification because of the belief that (1) if left undisturbed all vegetation not now climax would eventually be replaced by climax vegetation, hence seral communities are but stages in the development of the climax super-

organism, and (2) a single climax community is characteristic of each climatic region. This is a dynamic concept and shows the intrinsic ecological interrelations between all communities. Difficulties in its use and full acceptance are that the determination of the potential climax of a region is sometimes very difficult and theoretical, seral stages are often very extensive in area covered, subclimax communities close to but not actually climax climatically may be long enduring, and the climax vegetation may not actually be a single community but rather a mosaic of communities or a continuum which is dependent on differences in physiography, slope exposure, soil, or other factors that may be as permanent as climate and that modify the effect of climate in a secondary way.

In his forest classification for Canada, Halliday (1937) follows Weaver and Clements (1929) in putting emphasis on climaxes resulting from succession, but the plant communities recognized and his terminology are somewhat different.

Biotic communities

The biome concept employs the Clementsian philosophy of succession and climax for evaluating the interrelations of communities and develops a system applicable to animals as well as to plants. The basic unit of the system is not the "association," as described in the previous section, but the "plant-animal formation." The term "biome" is synonymous with formation and climax when these are used in the biotic sense. The development of this concept is largely the result of cooperation between F. E. Clements, the botanist, and V. E. Shelford, the zoologist (1939). They state (p. 20): "The plant-animal formation is composed of a plant matrix with the total number of included animals, of which the larger and more influent species may range over the entire area of the biome, including its subdivisions and developmental stages. The extent and character of the biome are exemplified in the great landscape types of vegetation with their accompanying animals, such as grassland or steppe, tundra, desert, coniferous forest, deciduous forest, and the like. These commonly represent biotic formations or climaxes, which in their general features have been noted by naturalists since the early days of biology." A map of the biomes in North America has been published by Pitelka (1941).

In developing a system of biotic communities, it is not sufficient to distinguish and describe the seral and climax plant communities of a region and then to list the animal constituents of each. This has resulted in the past in much confusion since animal species are often common in more than one plant community when these are distinguished by their species of plant dominants.

In order to define biotic communities properly, it is first necessary to determine what the true relations between plants and animals really are. A few species of animals, particularly insects, are closely dependent on particular species of plants for food or shelter, but the percentage of such species, even among insects, is very small. In general, the niche requirements of animals are not so refined that certain species of plants offer striking advantages over other species of similar life form. The concept is now becoming well-established, however, that animal species depend on, distinguish between, and respond to differences in life form of plants or in types of vegetation (Adams 1908, Trotter 1912, Dice 1923a, 1931, Moreau 1935, Pitelka 1941, Peterson 1942, Brecher 1943, Shelford 1945, Odum 1945, Kendeigh 1948). The basic fact in the biome concept is that there is agreement between the occurrence, distribution, and interrelations of animal species and types of vegetation but not necessarily with plant communities distinguished solely by the taxonomy of the plant dominants. This is true for the recognition of local biotic communities as well as geographic ones.

The term "biociation" has been proposed by the writer (Kendeigh 1948) as the designation of a climax biotic community with a distinct species composition of animals occurring in a particular type of vegetation or habitat. "Biocies" would be the equivalent term for a seral biotic community. It remains to be demonstrated whether species of subdominant plants as well as animals might not also fit better into distributional units like these than into associations and associes distinguished only by the species composition of the dominants.

In order to identify the particular biociation or biocies, the type of vegetation or habitat should be included in the name of the community. Furthermore when it is necessary to distinguish one community of animals and plants from another within the same type of vegetation or habitat, geographical names may be used or, as is done by plant ecologists, the names of two, conspicuous, characteristic, predominant animals. The type of vegetation or life form of the predominant climax organisms is enough to identify the biome by name.

The following example illustrates the use of this terminology as applied to a single biome:

Temperate deciduous forest biome
  European deciduous forest biociation
  Asiatic deciduous forest biociation
  North American deciduous forest biociation
    Seral communities:
    Deciduous forest-edge biocies
    Southern pine forest biocies
    Grassland biocies

Pond and marsh biocies
Stream biocies
Cristivomer—Tanytarsus lake biocies
Micropterus—Chironomus lake biocies

This is not the proper place for a detailed description of each of these communities or of the others that occur in North America (Fig. 8), but a few comments may be justified. The southern pine forest biocies may well have had greater distinctiveness and importance in ancient times than at present, since there is a characteristic group of animal species associated with it. At present, the community has become widely invaded by the deciduous forest biociation that outranks it successionally, and there is an interdiffusion of animal species between the two, especially in the belt mapped as ecotone.

The deciduous forest-edge biocies has a distinct composition of animal species, especially of birds and mammals, and hence is more than just an ecotone. It occurs as a seral shrubby stage in disturbed areas all through the area covered by the deciduous forest climax. Around the original borders of the forest, where the forest came in contact with grassland and ocean beaches, and in the aspen parkland to the north, the forest-edge

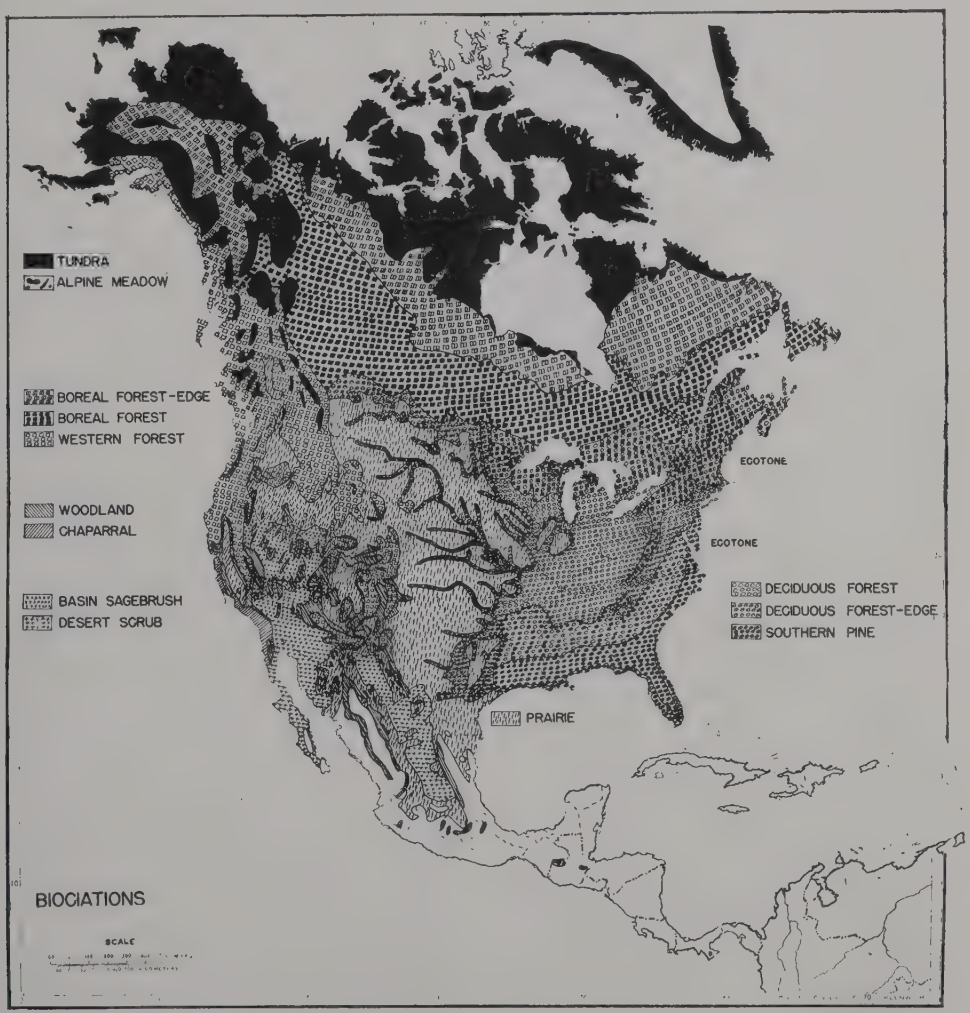

FIG. 8. Biociations of North America, together with the southern pine forest biocies. The deciduous forest-edge is essentially climax where shown but also extends as a seral unit throughout the eastern part of the continent. Ecotones are not distinct communities and hence are shown by overlapping the symbols of the adjacent communities.

was relatively stabilized climatically and might here be considered a biociation. The forest strips along rivers penetrating for miles into the grassland biome have some representative plants and animals of the deciduous forest biociation but are predominantly forest-edge in character.

The coniferous forest biome in North America has been separated into the boreal forest and western forest biociations largely on the basis of differences in the composition, habits, and past history of the bird populations present (Snyder 1950), but the separation appears also of importance to mammals. The coniferous-deciduous forest ecotone is not a distinct community since it is characterized by a mixture of species from the coniferous forest and deciduous forest biociations. The coniferous forest-edge in the north, however, does have many unique species and characteristics and is considered a separate biociation.

Each biociation and biocies has doubtless had a long and characteristic geological history. The tracing of the paleoecology of each community as a unit would be of great interest, particularly if it could be correlated with the evolution and differentiation of the individual plant and animal species involved. The biociations and biocies, although not necessarily continuous geographic areas, may represent major centers where species become differentiated and adapted to live in particular communities and habitats. Reconsideration of biotic provinces may show that they should be defined as subdivisions of biociations in which differentiation is proceeding at a lower taxonomic level.

The advantages of the biome system are several (Odum 1945, Shelford 1945):

1) The community units are readily recognized and named in the field from the vegetation type, principal plant dominants, species of predominant animals, or conspicuous indicator organisms.

2) The boundaries of the communities are more easily defined by vegetation type or prominent habitat differences than by overlapping of range boundaries of taxonomic units plotted on a map. Ecotones or transitional areas between communities that are adjacent either in space or time are generally recognized.

3) The communities are the expression and result of the effects of all interacting environmental factors, of succession dynamics, and of evolutionary development. The system of units is not based on the effect of any one or even a limited set of processes or factors.

4) The biotic community places emphasis on animal and plant populations. The quantitative measurement of sizes of populations per unit area is essential for locating a species in the community where it finds most favorable conditions and for interpreting and evaluating its role in the internal dynamics of the community.

5) The community with its complete ecosystem of animals, plants, and habitat is the natural unit for studying the interrelations, niche requirements, ethology, and evolution of its constituent species.

6) The biome system is flexible. Units may be added, combined, or eliminated as further research warrants. The system combines, for the determination of its hierarchy of units, criteria used by students of floristics, faunistics, vegetation, plant sociology, and community dynamics and could be logically developed to serve as a synthesis of these various points of view.

Summary

1. Serious study of animal and plant distribution began during the late eighteenth century with the work of Georges L. L. Buffon and Alexander von Humboldt.

2. The development to modern times of the floristic concept of communities is traced for North America through the work of Schouw (1823), Pickering (1830), Candolle (1855), Gray (1856-57, 1880), Engler (1882), Drude (1884, 1887, 1890), Sargent (1884), and Harshberger (1911).

3. The study of vegetation or physiognomy of landscapes, as distinct from floristics, is traced from Humboldt through Meyen (1836), Berghaus (1838), Cooper (1859), Grisebach (1872), Engler (1882), Drude (1884, 1887, 1890), and Schimper (1903).

4. There were many students of faunistics during the past century of whom the following made noteworthy contributions: Wagner (1846-51), Agassiz (1845, 1854), Amos Binney (1851), Woodward (1851-56), Schmarda (1853), Sclater (1858), Le Conte (1859), Verrill (1864, 1866), Baird (1866), Murray (1866), W. G. Binney (1873), Cope (1875), Wallace (1876), Packard (1883), Heilprin (1887, 1897), Allen (1871, 1878, 1892, 1893), and Merriam (1890, 1891, 1892, 1898, 1910).

5. Several students of floristics or faunistics attempted some incidental comparisons between the distribution of plants and animals, but perhaps Berghaus (1838), Wagner (1846-51), Schmarda (1853), and especially Cooper (1859) need to be mentioned in this connection. The synthesis of a biotic point of view in the study of distribution is largely a development of the twentieth century.

6. Modern floristic and faunistic studies are concerned with interpreting the distribution of taxonomic units in regard to geological origin, dispersal pathways, phylogenetic relations, and evo-

lution, and the control over these phenomena exerted by climate, soil, topography, and continental configurations. A recent trend is, before describing geographic areas, to analyze floras and faunas into floral elements and faunal groups which include species with similar climatic and biotic tolerances, ranges, and evolutionary histories.

7. Studies of vegetation involve analysis of physiological relations of plants to their environment, morphological adjustments in life form, and the structure of the resulting communities that are formed.

8. Life-zones continue to be useful geographic units in the western mountains, particularly when they agree with types of vegetation, but are criticized in their general application, a) because they group together into transcontinental belts widely varying types of vegetation, flora, and fauna, b) because they overemphasize the controlling role of the single factor of temperature, and c) because they are broad static geographic units that are not intended for analysis of communities or habitats of more local or restricted occurrence.

9. Biotic provinces, in actual practice, are continuous geographic areas exhibiting a differentiation and distinctness of fauna at the species and subspecies level. Their recognition requires extensive collecting and taxonomic comparison of specimens from neighboring regions.

10. Associations are communities of plants recognized by the distinctiveness in taxonomic composition of the more conspicuous or dominant species. Associations are often grouped together, depending largely on the life-form of the more important species, into formations. Difficulties in the use of climax associations as the basis of a geographical system of plant distribution is the frequent uncertainty in regard to the climatic climax, in the persistence over long periods of time of some late seral stages, and the complex faciation of the climatic climax on different topographical or soil sites.

11. In the biome concept, both animals and plants are included and in terrestrial habitats the climax type of vegetation and not the association delimits the basic unit, the biome, since differences in vegetation require distinct adjustments of animals in morphology, physiology, and behavior. Major subdivisions of the biomes are the biociations, each of which has a distinct species composition that has become differentiated due to isolation and evolution. Biocies are equivalent seral biotic communities. Both biociations and biocies on land may include more than one plant association or associes provided they are of the same type of vegetation.

12. The biome system, in its hierarchy of units, makes use of criteria, procedures, and objectives of students of floristics, faunistics, vegetation, plant and animal sociology, and community dynamics and could be further developed to serve as a common synthesis of these various points-of-view.

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ESTABLISHMENT AND FOOD HABITS OF THE NUTRIA IN TEXAS[1]

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The nutria (*Myocastor coypu*) has been an object of considerable interest and discussion during the past few years. Ashbrook (1948) discussed importations from their native rivers, estuaries, and marshes of South America to fur farms in Germany, Switzerland, France, Canada, Russia, and the United States. In this discussion Ashbrook also related how many of these animals escaped or were released into the wild due to financial failure of the fur farmers. Atwood (1950) reported on the life history of this exotic in the coastal areas of Louisiana.

Those occurring in Texas are descendents of animals imported by E. A. McIlhenny to Avery Island, Iberia Parish, Louisiana in 1937. Dallas fur buyers have reported that as early as 1946 a few nutrias were trapped along the coast near Port Arthur, in southeastern Texas, but apparently there was no appreciable natural spread of this species inland. In April of 1946, Mr. A. C. Lively, reportedly with the intention of growing nutrias for their fur, obtained 20 females and four males from Avery Island and released them in a 300-400 acre marsh near Slocum, Anderson County, 160 miles inland from Port Arthur. About the same time Mr. C. N. Campbell, a relative of Mr. Lively, released three animals into a small five-acre pond near Grapeland in Houston County (Petrides 1950).

The outcome of the introductions into Mr. Campbell's pond seemed to be the impetus behind wholesale introductions in 1949 and 1950. According to Mr. Campbell and his neighbors, the pond into which the nutria were released was practically filled with vegetation in 1948 when they were first introduced. By the summer of 1949 it became apparent to the importer that there was much less vegetation in his pond, a condition which he attributed to the activities of the nutria. Since Texas pond owners frequently encounter difficulty in controlling aquatic and semi-aquatic vegetation in impoundments, Mr. Campbell began selling nutrias on the strength of their apparent ability to remove undesirable water weeds. The supply of nutrias from Mr. Campbell's small pond was not sufficient to meet the demand, so he imported more from Louisiana. He later bought out trapping rights in the Slocum Marsh from Mr. Lively in order to supplement his supply from Louisiana. By August, 1950, we determined through conversations with Mr. Campbell that releases of nutrias had been made in 21 counties (Fig. 1) and there were probably others that Mr. Campbell did not recall during our conversations. Approximately 195 animals, supposedly released in each area at a ratio of about two females to each male, were placed in recreational and stock water impoundments and in southeastern coastal marshes.

[1] This study was conducted while the senior author was Instructor of Wildlife Management, A. & M. College of Texas, and the junior author was Leader, Texas Cooperative Wildlife Unit, College Station, Texas.

INFLUENCE OF NUTRIAS UPON VEGETATION

During this investigation, studies were made of 11 ponds in which nutrias had been released. The areas were visited three times each year; in May, August, and January of 1949-50 and 1950-51. Notes were made concerning changes in vegetation and evidence of nutria activity. At each visit photographs were taken to record any changes in vegetation.

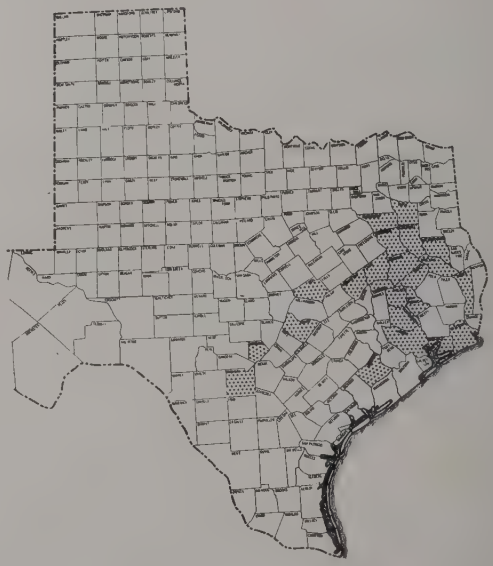

FIG. 1. Dotted areas are Texas counties into which nutrias had been released up to August 1950.

Nutrias readily eat cattail (*Typha latifolia*) shoots and roots. Typically, they "clear cut" almost all stems in a small area rather than feed on stems over a wider area. Three nutrias, reportedly one male and two females, were introduced into Elmore Lake, San Jacinto County, in November, 1949. By January 24, 1951, the nutria population had almost eliminated a ¾-acre patch of cattail at the upper end of the lake (Fig. 2). Most of the stalks had been cut just below the waterline, and only the underwater and basal portions had been utilized as food. Many of the stalks lay where they had been cut, but others had been pulled together to form numerous feeding platforms (Fig. 3). As long as the supply of cattail lasted, very few other species of plants were utilized for food.

FIG. 2. An "eat out" area at the upper end of Elmore Lake. Vegetation predominantly cattail. Note cut material under the surface of the water.

FIG. 3. Nutria feeding platform, Elmore Lake, August 1950.

Water shield (*Brasenia schreberi*), which covered most of the pond's surface, held little attraction as food, although an occasional one was found with a floating leaf neatly clipped off as though it had been done to reduce interference to travel. From the standpoint of pond owners desiring open water, this plant was one of the most obnoxious for it extended far into the middle of most ponds, sending its floating leaves to the surface from depths of up to seven feet. Water shield occurred on practically all areas studied, and nowhere was there a noticeable reduction in its abundance which could be attributed to nutria activity.

Giant cutgrass (*Zizaniopsis milacea*) was another preferred item in the diet of the nutria. In Slocum Marsh, one of the original release areas, a ten-acre segment completely surrounded by a dense stand of tall and coarse *Zizaniopsis* was evidently cleared by nutrias whose signs were everywhere (Fig. 4). In May, 1950 (Fig. 4b), the dominant plants in the area free of giant cutgrass were bulrush (*Scirpus* sp.) and arrow arum (*Peltandra virginica*). These were largely replaced in August (Fig. 4c) by rice cutgrass (*Leersia oryzoides*) and arrowhead (*Sagittaria* sp.) apparently due to normal seasonal succession. Plants occurring there in less abundance were frog-fruit (*Lippia* sp.) and a panic-grass (*Panicum* sp.). By January, 1951 (Fig. 4d), most of the rice cutgrass plants had died down leaving the area covered with their dry remains. Many nutria cuttings of giant cutgrass shoots and roots were observed. The animals also seemed to relish the stems and rootstocks of arrowhead and the tender succulent growths of *Panicum*. Only a few leaves of the rice cutgrass and a few *Scirpus* tops were eaten. Arrow arum was ignored. January photos for 1951 (Fig. 4d) and 1950 (4a) indicate little total change in vegetation during the intervening year.

The roots of white water lily (*Nymphaea elegans*) were taken occasionally as food. On Warner's Pond west of Grapeland, roots and stems frequently were found floating in the water with tooth marks plainly visible where they had been cut off by nutrias. Some small areas were cleared temporarily of water lily foliage. Some water milfoil (*Myriophyllum* sp.) stems were observed floating free in this pond, but it was not determined whether the nutria had used this species as food, or had merely removed the material from runways in shallow water.

Roots and new shoots of pickerel weed (*Pontederia cordata*) were consumed intensively in Normangee Lake, Madison County. Evidence that nutria were particularly fond of this plant was noted during a visit in February, 1950, as they were consuming in great quantities the new growth abundant at that time. In addition, giant cutgrass, abundant at this site, was much cropped.

Although some plant species occurred in abundance on several of the areas studied, they were used little or not at all. Among those particu-

FIG. 4A. A large area in Slocum Marsh cleared of giant cutgrass by nutria. January 1950.

FIG. 4B. Same photo point, May 1950. Bulrush and arrow arum were dominant plants.

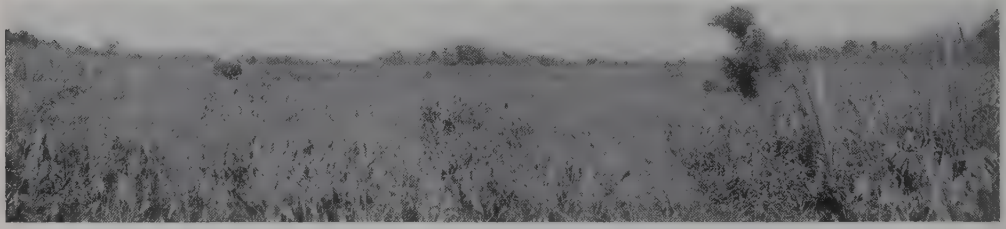

FIG. 4C. Same photo point, August 1950. Dominant plants were rice cutgrass and arrowhead.

FIG. 4D. Same photo point, January 1951. Dominant vegetation was rice cutgrass. Note only slight change from January 1950 conditions.

larly noticeable, in addition to arrow arum and water shield previously mentioned, were American lotus (*Nelumbo lutea*) and smartweed (*Polygonum* sp.).

It is still uncertain whether nutrias will turn from preferred foods such as cattail to such little-used species as water shield as their population increases or whether they will move to other areas containing more desirable food species.

Burrowing Activities

Burrows of nutrias (Laurie 1946) were found at only two study areas. However, in each case there was only one tunnel and it showed limited use. The preferred nesting places were "beds" beneath dense overhanging or collapsed marsh vegetation. Areas where young nutrias were reported were thoroughly searched with no other "home" structures being detected. At Lake Normangee, where young nutrias were reported by reliable persons, many nutria trails were followed but no dens were found. From these data it is concluded that more elaborate den sites are not necessary and that nutrias may rest, feed, and probably give birth to young in these crude and more or less open "forms." Damage to ponds has been reported, however, as a result of burrowing.

Economic Status

Predictions as to whether nutrias eventually

will be beneficial or detrimental have now lost much of their usefulness, as it appears that this animal is already permanently established in North America. Ashbrook (1948) reported feral nutrias in the states of Oregon, New Mexico, Oklahoma, Michigan, and Iowa, and says that they are rather well established in the states of Washington, Louisiana, and Texas. Petrides and Leedy (1948) recorded a feral nutria from Ohio in 1946.

In Louisiana the fur value of the nutria at present seems to exceed the damage done by them. In 1950-51 trapping season some 78,000 nutrias were pelted. Furthermore, during some years, as from 1948 to 1951, muskrat populations were low and nutrias provided a much-needed source of income for trappers. In 1950-51 large Louisiana nutria pelts brought from $2.00 to $6.50 and averaged about $4.65 (mimeographed release of Louisiana Department of Wildlife and Fisheries, undated). There seems to be little direct competition between the muskrat and nutria in Louisiana, for there muskrats occupy chiefly brackish marshes while nutrias prefer freshwater areas (Atwood 1950). There has been some encroachment into what is considered secondary muskrat habitat which produces a trappable surplus about two years out of five (personal communication from John Lynch, U. S. Fish and Wildlife Service, Abbeville, Louisiana).

In the rice fields of Louisiana, nutrias have been a source of some trouble. They have dug holes in the levees of irrigation canals to such an extent that water companies must have crews to trap or dig them out. After the animals have been removed the burrows must be filled in to prevent leakage during the rice planting season. Furthermore, since there is little vegetation in these canals, nutrias move out into the fields at night to eat growing rice plants.

In Texas, nutrias along the coast have not reached a sufficiently high population level to indicate conclusively their ultimate status, but in all probability conditions there eventually will be similar to those now prevailing in Louisiana. Inland in Texas, the muskrat occurs only in the eastern half of the Panhandle and locally along the Rio Grande and Pecos Rivers (Taylor and Davis 1947). This means that in an area of about 267,000 square miles, containing an estimated 200,000 impoundments, and much of it crossed by numerous deeply intrenched and highly variable streams, there exists a habitat, especially in impoundments, that from all appearances is quite similar to that occupied by the muskrat throughout other parts of the United States. But in Texas this habitat appears to be unfilled. The nutria will probably increase rapidly in this area and provide an additional source of income as a fur-bearer and perhaps as an agent in partial control of aquatic weeds.

Also in Texas nutrias have already begun to make an impression as pests. They have been accused of making depredations upon corn, cabbage, and sugar cane, and at least one pond has been destroyed by their burrowing into an earthen dam. In the Palestine, Texas, area a newspaper account reports that the nutrias "dug holes in the 15-foot embankment between . . . lakes." It further advises that the animals "spend too much time running around to nearby gardens and roasting-ear corn patches instead of tending to the business of cleaning out lakes."

Elsewhere in the United States, nutrias that may become established doubtless will compete with muskrats for food and cover. In Washington and Oregon (Hale 1950) they already are believed to be detrimental to muskrat populations and have yielded only low fur values.

Like many imported species it seems likely that the nutria will be a mixed blessing. It has some fur values and, at least in Louisiana, is of considerable worth. Elsewhere, however, it seems probable that its destructive tendencies will often outweigh its good qualities. Especially as it spreads northward and inland it can be expected to become increasingly troublesome to landowners in agricultural areas and to muskrat marsh operators and trappers.

Summary

Prior to August, 1950, the nutria was introduced into at least 22 counties in Texas. A survey of their food habits in freshwater impoundments indicates that they readily eat cattail, giant cutgrass, arrowhead, panic-grass, white water lily, and pickerel weed. To a lesser extent rice cutgrass was eaten. Arrow arum, water shield, American lotus, and smartweed occurred on the areas studied, but were not used as food. The animals tend to "clear cut" almost all stems in a small area, thereby making openings in an otherwise vegetation-choked marsh. Little evidence of burrowing was noted. The nutrias seemed to use open "beds" or "forms" for their homes. The eventual economic desirability of this rodent, especially inland in agricultural areas, is debatable. Regardless of its final status it is apparently now rather permanently established in part of Louisiana, Texas, and other states.

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PLANT SUCCESSION AND YIELD OF LIVING PLANT MATERIAL IN A PLOWED PRAIRIE IN CENTRAL OKLAHOMA[1]

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At the University of Oklahoma in the winter of 1949-1950, a five-year program of grassland research was outlined with emphasis on the effects of mulching and plowing. Unfortunately, in January, 1952, a devastating fire jumped the protecting firebreak, spread over all of the plots, completely eliminated the mulching studies, and modified the other plots considerably. Although no reports were contemplated until the end of the five-year period, it is deemed desirable to present some of the more interesting changes that occurred previous to burning. This is particularly true since the amount of living areal cover produced during the second growing season after plowing was approximately two and one-half times as great in each of the plowed plots as in the control. This paper presents a comparison of plant succession, plant production, and certain physical factors in three half-acre plots: unplowed native prairie (control); plowed, unmulched prairie; and plowed, mulched prairie.

METHODS

In December, 1949, the grass was mowed and raked from one acre of tall-grass prairie in the University of Oklahoma Grassland Plots located eight miles southwest of Norman, Oklahoma, on Highway 9. The mowed plot was then plowed and disked, and the prairie hay which had been removed was applied in January, 1950, as a surface mulch to one-half the plot at the rate of 6,000 lbs. per acre. The other half was left unmulched. An area one-half acre in extent immediately adjacent to the plowed area was designated as the control plot. None of the area involved in the present experiments had ever been plowed. Grazing had been extremely light for many years, and none had occurred after the summer of 1949. A detailed study of all three plots in the fall prior to the beginning of the experiment showed that the vegetation of all plots was similar.

The vegetation was sampled in each of the three one-half acre plots indicated above in May, 1950; August, 1950; and August, 1951. Twenty-five 0.1 sq. m. quadrats were analyzed in each plot for frequency and areal living cover (expressed in per cent of quadrat area) of each species present. Two area gauges were available to facilitate the estimation of areal cover, one representing 1% and the other representing 5% of the total quadrat area. After the above analysis in each quadrat, all plant material was clipped for subsequent determination of the oven-dry weight of living and of dead cover in each plot.

To determine the relative concentrations of roots and rhizomes in the top seven inches of soil in the plowed (plowed 7 inches deep) versus the control plot, five blocks of soil, each 14 inches long, 6 inches wide, and 7 inches deep were removed from the mulched plowed plot and five similar blocks from the control in May, 1952. The subterranean parts contained in the blocks of soil were carefully washed, dried in a forced draft oven, and weighed.

Soil samples for the determination of organic carbon were taken from three levels in the plowed plots: 0-6, inches, 6-12 inches, and 12-18 inches. In the control, samples were taken from just the first and third levels. Organic carbon (Walkley and Black method) was determined by the method outlined by Piper (1944). In the preparation of the soil samples for the above determinations, all organic matter was thoroughly ground and mixed with the rest of the sample. The numbers of samples analyzed and the dates of sampling are given in the tables of results.

The precentage of soil moisture based on the oven-dry weight of the soil was determined for the 0-6 inch and 12-18 inch levels at irregular intervals in all plots. Four to six samples were

[1] First in a series of papers from the Grassland Investigations Project, on land provided by Mr. Neil R. Johnson. This investigation was supported in part by grants from the University of Oklahoma Faculty Research Fund.

taken at each level in each plot at each sampling period.

To determine the volume-weight of the soil, a small hole approximately two inches in diameter and three inches deep was made, and all the excavated material was taken to the laboratory for oven-dry weight determination. The volume of the hole was then determined by pouring dry sand into it from a graduated cylinder and noting the volume used. The volume-weight was calculated by dividing the oven-dry weight (in grams) of the excavated soil by the volume of the soil (in c.c.). Six to ten measurements were made in each plot at each sampling period.

Results

Vegetation

The dominant plants in the control plot in May, 1950, based on cover and frequency were *Andropogon scoparius,*[2] *A. gerardi, Sorghastrum nutans,* and *Panicum virgatum* (Table I). At the same time, the dominants in the unmulched plowed plot were *Ambrosia psilostachya* and *Oxalis violacea* with *P. virgatum* as an important secondary species (Table I). The dominants in the mulched plowed plot on the above date were *A. psilostachya* and *P. virgatum* (Table I). The frequency of *A. psilostachya* was considerably greater in the unmulched than in the mulched plot at this sampling period.

Table I. *Effect of plowing on living areal cover (%) in the prairie. Plowed December, 1949; mulched January, 1950; sampled May, 1950. Each entry is average of 25 quadrats with standard error*

Species†	Control	Plowed-Mulched	Plowed-Unmulched
Andropogon scoparius	8.2±2.5	t	t
Andropogon gerardi	8.1±1.9	0.5±0.3	0.1±0.08
Sorghastrum nutans	3.4±1.0	0.2±0.02	0.2±0.1
Panicum virgatum	2.6±0.5	1.2±0.4	1.3±0.4
Leptoloma cognatum	t	none	none
Ambrosia psilostachya	0.5±0.2	1.6±0.8	3.6±1.0*
Panicum scribnerianum	0.3±0.2	0.1±0.04	0.7±0.2*
Oxalis violacea	0.1±0.08	0.5±0.1	3.0±1.0*
Number of species in quadrats	32	19	23
Average living cover of all species	33.6	6.1	11.9

†Only those species included which were considered dominant in at least one plot at some sampling period.
*Frequency more than double control.

By August, 1950, the same species were prominent in the control as in May (Table II). *A. psilostachya* was the only species which could be considered dominant in the unmulched plowed plot although the average cover percentages of *Leptoloma cognatum* and *P. virgatum* were approximately the same as in the control (Table II). *A. psilostachya* and *P. virgatum* were still the dominants in the mulched plowed plot. In August, 1950, the average cover of the latter species was approximately twice as great in the mulched plowed plot as in the control, and the frequency was somewhat higher also. The average cover of *A. psilostachya* in the mulched plowed plot was significantly less (.05 level) than in the unmulched plowed plot on the above sampling date.

Table II. *Effect of plowing on living areal cover (%). Same plots as in Table I. Sampled in August, 1950. Each entry is average of 25 quadrats with standard error*

Species	Control	Plowed-Mulched	Plowed-Unmulched
Andropogon scoparius	11.9±2.2	1.0±0.4	0.8±0.5
Andropogon gerardi	11.7±1.8	2.0±1.0	1.7±0.8
Sorghastrum nutans	8.1±1.8	0.3±0.1	0.5±0.2
Panicum virgatum	8.1±1.4	18.4±3.6†	7.2±1.7
Leptoloma cognatum	3.6±0.7	4.8±2.2	4.4±1.0
Ambrosia psilostachya	1.8±0.8	34.2±5.9*	50.0±4.5*
Panicum scribnerianum	0.6±0.2	2.2±0.6*	4.0±1.3*
Number of species in quadrats	20	25	27
Average living cover of all species	51.3	70.3	77.1

†Frequency somewhat higher than that of control.
*Frequency at least twice that of control.

By August, 1951, the average cover of *A. psilostachya* had fallen to less than one per cent in both plowed plots (Table III). By that date, all of the important species in the control had become important in the plowed plots. In fact, the average cover of *P. virgatum* was approximately twice as great in the unmulched plowed plot and about four times as great in the mulched plowed plot as in the control. Moreover, the average cover of *Leptoloma cognatum* was several times as great in each of the plowed plots as in the control (Table III). The cover of *Panicum scribnerianum* was also significantly higher (.01 level in unmulched and .05 level in mulched) in each of the plowed plots than in the control. The total average living cover of all species was approximately two and one-half times as great in each of the plowed plots as in the control in August, 1951.

In May, 1950, the amount of living material based on oven-dry weight was significantly less in both plowed plots than in the control plot (Table IV). By August, 1950, the weights of living material were essentially the same in all three plots, none of the differences being significant. By August, 1951, the yield of living material was significantly greater in each of the plowed plots than in the control (Table IV).

[2] All nomenclature of the grasses is according to Hitchcock and Chase (1950); that of other species follows Fernald (1950).

TABLE III. *Effect of plowing on living areal cover (%). Same plots as in Table I. Sampled in August, 1951. Each entry is average of 25 quadrats with standard error*

Species	Control	Plowed-Mulched	Plowed-Unmulched
Andropogon scoparius	14.8±1.8	9.2±1.7	10.0±2.4
Panicum virgatum	9.7±2.1	42.3±2.0*	20.8±2.8*
Andropogon gerardi	6.1±1.3	11.8±3.6	2.8±1.2
Sorghastrum nutans	4.7±1.0	8.3±3.2†	7.5±1.5†
Leptoloma cognatum	2.9±1.2	27.7±4.7*	42.8±4.9*
Panicum scribnerianum	0.5±0.05	4.3±1.7*	9.1±1.8*
Ambrosia psilostachya	none	0.5±0.2	0.1±0.08
Number of species in quadrats	18	24	26
Average living cover of all species	42	110	106

*Percentage frequency much higher than control.
†Percentage frequency about same as control.

In May, 1952, the oven dry weight of all roots and rhizomes to a depth of seven inches was 5112.8 ± 835.8 pounds per acre in the control, and 4965.4 ± 852.1 pounds per acre in the mulched plowed plot. The difference was not statistically significant.

TABLE IV. *Effect of plowing on oven-dry weight of living material (lbs./acre). Each entry is average of 25 quadrats with standard error*

Plot	May, 1950	Aug., 1950	Aug., 1951
Control	1654±143	4264±258	3060±250
Plowed-Mulched	112±36†	4640±340	5656±553†
Plowed-Unmulched	288±15†*	4770±402	4639±410†

†Difference from corresponding control significant at .01 level.
*Difference from value in mulch plot significant at .01 level.

Soil factors

The volume-weight of the soil in the mulched plowed plot in May, 1950, was significantly greater than that in either the control plot or the unmulched plowed plot (Table V). On that date, the volume-weight of the soil in the unmulched plowed plot was not significantly different from that of the control. In October, 1950, the volume-weight of the soil in the mulched plot still appeared to be slightly greater than in either of the other plots but none of the differences was significant (Table V).

TABLE V. *Effect of plowing on volume-weight of soil. Each value based on 10 samples excepting plowed plots on May 3, 1950, which were based on 6 samples each*

Plot	Date of sampling		
	May 3, 1950	Oct. 29, 1950	March 24, 1951
Control	1.1±.05	1.0±.11	1.1±.04
Plowed-Mulched	1.3±.07†	1.2±.04	1.0±.05
Plowed-Unmulched	1.0±.07*	1.1±.05	1.0±.04

†Difference from control significant at .05 level.
*Difference from value in mulch plot significant at .01 level. Not significantly different from control.

The average percentage of soil moisture was consistently less in the unmulched plowed plot than in either the mulched plowed plot or the control (Table VI). With few exceptions, the differences were statistically significant in both the 0-6 inch and the 12-18 inch levels in the soil. Excepting the 0-6 inch level on two sampling dates, the average percentage of soil moisture in the mulched plowed plot was lower than in the control (Table VI). Although the differences were statistically significant on only two occasions, the fairly consistent trend suggests slightly less desirable soil moisture conditions in the mulched plowed plot than in the control.

The data on organic carbon of the soil were quite variable among the three plots (Table VII). The most striking change during the growing season of 1950 was the rapid decrease in organic matter in the 6-12 inch level in the plowed plots. The rate of decomposition appeared to be greater

TABLE VI. *Soil moisture (%). Each entry for control is average of 6 samples with exception of entries for July 29, 1951. Each entry for* mulch *and* no mulch *plots up to April 4, 1951, is average of 4 samples. Each entry for those plots on April 4, 1951, is average of 6 samples. Each entry for July 29, 1951, is average of 5 samples. (Standard errors included)*

Plot	April 19, 1950		June 27, 1950		Sept. 6, 1950	Nov. 2, 1950		April 4, 1951		July 29, 1951	
	0-6″	12-18″	0-6″	12-18″	0-6″	0-6″	12-18″	0-6″	12-18″	0-6″	12-18″
Control	20.7±.7	17.4±.5	15.6±1.3	16.0±.3	13.8±1.2	12.4±1.0	15.2±.8	21.9±.7	18.7±.6	13.1±.7	10.1±.2
Plowed-Mulch	22.4±1.2	17.3±.1	14.5±1.4	15.7±.9	11.2±.5	9.7±.8	11.5±.6 †	19.3±.6 †	17.6±.4	13.5±2.0	10.0±1.0
Plowed-No Mulch	19.4±.8	16.5±.2 *	7.3±1.3 *†	9.2±.9 *†	6.9±.9 *†	5.6±1.2 *†	7.2±.5 *†	15.0±1.2 *†	15.7±.3 *†	12.4±.8	9.8±.7

*Difference from corresponding value for mulch plot significant at .01 or .02 level.
†Difference from corresponding control significant at .01 or .02 level.

TABLE VII. *Organic carbon (%) (Walkley and Black values). Each entry is average of 6 samples with standard error. Plots plowed in December, 1949, about 7 inches deep*

Plot	April 25, 1950			Nov. 19, 1950		
	0-6″	6-12″	12-18″	0-6″	6-12″	12-18″
Control	1.26±.05	.....	.61±.03	1.14±.05	.....	.53±.02
Plowed-Mulched	1.44±.06	.99±.10	.71±.02	1.18±.09	.60±.03	.49±.02
Plowed-No Mulch	1.10±.19	.95±.08	.66±.05	1.03±.04	.74±.05	.55±.04

at all levels in the mulched plowed plot than in the corresponding levels of the other plots (Table VII).

DISCUSSION

Booth (1941) found that succession in abandoned fields in central Oklahoma included annual weed, annual grass, perennial bunch grass, and true prairie stages. He found that the fully developed prairie stage was not attained in 30 years. Smith (1940) reported the following successional stages in abandoned fields in central Oklahoma: mixed weed, annual grass (with three substages), subclimax, and climax prairie. In the plowed prairie plots, perennial forbs and dominant climax grasses appeared in the spring of the first growing season. None of the first three stages described by Booth (1941) or Smith (1940) was present in the plowed prairie plots. By the end of the second growing season, the major perennial forb, *Ambrosia psilostachya,* had nearly disappeared and the climax prairie was closely approximated. The major reason for the rapid recovery of the prairie in the present project was the presence of living perennating parts in the soil from which the dominant species could start anew.

The chief effect of the mulch was to inhibit the growth of *A. psilostachya.* This inhibition probably favored the growth of *P. virgatum* since the cover of the latter species was approximately twice as great in the mulched plowed plot as in the unmulched plowed plot at both August samplings.

Whittet (1944) reported that the yield of *Paspalum dilatatum* swards in New South Wales, Australia, increased 127% during the first year after plowing and 70% the second year. Fletcher (1950) reported considerable increases in carrying capacity of *Phalaris tuberosa* pastures in Australia as a result of moldboard plowing followed by harrowing and surface seeding with red and white clover. In England, the practice of plowing up permanent grasslands and reseeding them has been widely adopted because of the large increases in yields which result during the first few years after plowing (Bates 1948).

A very careful survey of all appropriate abstracting journals and indices of federal and state publications indicates that virtually nothing has been done on the effects of moldboard plowing on yields from grasslands in the United States. Ten years after ripping a desert grassland plot near Elgin, Arizona, with subsoiling chisels, Brown and Everson (1952) found that the ripped area produced 2.5 times more grass than the adjacent non-ripped area. Increased water penetration and storage due to the ripping operation were probably the chief causes of the increased yield. Heady (1952) reported that disking or disking plus spring toothing promoted increases in yield of grasses in the relic mixed prairie on the North Montana Branch of the Montana Agricultural Experiment Station near Havre, Montana. He found, however, that manuring improved yields more than did disking or disking plus spring toothing. Harper (1948), without citing any experimental results, stated that the forage-producing capacity of sod-bound pastures composed principally of Kentucky bluegrass, bromegrass, or Bermuda grass can be increased by early spring tillage. His explanation for such an increase was that "stirring the soil hastens the decay of organic matter and indirectly provides more nitrogen and other nutrients for plant growth." Bradfield (1948) pointed out that the amounts of nitrogen required to produce maximum yields of forage grasses is quite large and that old grass sods are frequently deficient in readily available nitrogen. In general, it appears that most agronomists and soils men feel that the chief cause of low yields of forage in old grass sods is a deficiency of available nitrogen.

Bates (1948) believed, however, that the decline in yield in sodbound pastures in England was due to the "accumulation of a mat of dead root material below the soil surface and an increase in the number of tillers" resulting in "a crowded condition and consequent dwarfing and loss of vigour in the grasses. . . ." He did suggest that a loss of plant nutrients from the soil might be a contributing factor in some cases.

In the present project, it seems very doubtful that the tremendous increases in areal cover and yield of living material in the plowed areas in the

second growing season after plowing were due to the elimination of a sod-bound condition in the sense described by Bates. As previously pointed out there was no significant difference in oven-dry weight of roots and rhizomes between the control and the mulched plowed area shortly after the beginning of the third growing season after plowing. Plowing apparently did not bring about the increase in yield by a loosening of the soil because the only change in volume-weight which was statistically significant was an increase in the mulched plot (more compact soil) during the first spring following the plowing. Moreover, the soil moisture content was nearly always lower in the plowed plots than in the control. The most logical postulation, based on present evidence, is that the increase in yield was due chiefly to the greater availability of minerals, particularly nitrogen, in the plowed plots resulting from a decomposition of the large amount of organic matter which was plowed under. The explanation suggested above is, of course, in agrement with the theory generally held by agronomists and soils men that the sod-bound condition in grasslands is largely due to a deficiency of available nitrogen.

Summary

The present paper presents a comparison of plant succession, plant production, and certain physical factors in three half-acre prairie plots near Norman, Oklahoma: unmulched, plowed; mulched, plowed; and unplowed (control).

Andropogon scoparius, A. gerardi, Sorghastrum nutans, and *Panicum virgatum* were the dominants in the control plot during the period of this investigation. The first plants to appear in the plowed plots were perennial forbs and perennial grasses. At the end of the first growing season after plowing, *Ambrosia psilostachya* was the most important *dominant* in both plowed plots

By the end of the second growing season, all of the dominants in the control were prominent in the plowed plots, and *A. psilostachya* had nearly disappeared in all plots. Succession back to the prairie stage was, therefore, extremely rapid under the conditions of the experiment.

The chief effect of the mulch was to inhibit the growth of *A. psilostachya*.

The amount of living areal cover produced during the second growing season after plowing was approximately two and one-half times as great in each of the plowed plots as in the control.

The oven-dry weight of living material produced (above-ground) during the second growing season was significantly greater in each of the plowed plots than in the control.

The increases in yield in the plowed plots were apparently not caused by a loosening of the soil because the only change in volume-weight which was statistically significant was an *increase* in the mulched plot during the first spring following the plowing.

The soil moisture content was nearly always lower in both plowed plots than in the control.

The data on organic carbon of the soil were quite variable among the three plots. The most striking change during the first growing season was the rapid decomposition of organic matter in the 6-12 inch level in the plowed plots.

The oven-dry weight of all subterranean parts to a depth of seven inches (the depth of plowing) in the mulched plowed plot was not significantly different from that in the control plot. These data suggest that the increases in yield in the plowed plots were not due to an elimination of a sod-bound condition in the sense of Bates (see text).

The most logical postulation at present for the increase in yield due to plowing is that it was due chiefly to the greater availability of minerals, particularly nitrogen, resulting from the decomposition of the large amount of organic matter which was plowed under. This suggested explanation is in agreement with the theory most generally held by agronomists and soils men that the sod-bound condition in grasslands is largely due to a deficiency of available nitrogen.

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BODY TEMPERATURE AND WATER REQUIREMENTS IN THE MOURNING DOVE, *ZENAIDURA MACROURA MARGINELLA*[1]

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The problems of regulation of body temperature and maintenance of water balance are particularly acute for most desert birds because they are exposed to intense heat under conditions of great aridity. As a contribution to the understanding of the adjustment of birds to desert conditions, we have investigated the body temperature and water requirements of the western mourning dove, a common resident of central and western United States and Mexico, and one of the most abundant breeding birds in the deserts of California. We have examined (1) body temperature in the presence and in the absence of heat stress, (2) the differences in temperature between different parts of the body at various environmental temperatures, (3) the effects of temperature on water consumption, and (4) the effects of water deprivation on body temperature. In addition we have attempted to evaluate the ecological significance of our laboratory studies by observing the behavior of mourning doves under natural conditions.

MATERIALS AND METHODS

Mourning doves weigh approximately 120 grams. They feed almost exclusively on seeds and are easily obtained with conventional bird traps. The birds used in the present study were trapped on the Los Angeles Campus of the University of California, which, because of its proximity to the ocean, has cooler summers and warmer winters than the nearby Mohave and Colorado deserts. Consequently our physiological data were obtained from birds which do not themselves meet extreme desert conditions. However, since mourning doves are distributed without interruption from the Los Angeles Basin into the nearby deserts, we assume that there are no important physiological differences between the birds we studied and those occupying the adjacent desert areas.

All temperatures were measured with silver-soldered thermocouples made of duplex 30-gauge copper-constantan wire coated with baked insulating enamel. Temperatures were recorded to the nearest tenth of a degree centigrade on a Brown strip chart recording potentiometer. A stepping switch driven by a synchronous electric motor allowed us to record both the body temperature and the air temperature.

The continuous long-term temperature records were obtained from thermocouples which had been filed to a point, inserted into the pectoral muscle between the keel of the sternum and the left ventral feather tract, and held in position as shown in Figure 1. Prior to surgery the birds were anesthetized with an intramuscular injection of sodium pentobarbital. A 1:1000 aqueous solution of benzalkonium chloride was used as an antiseptic.

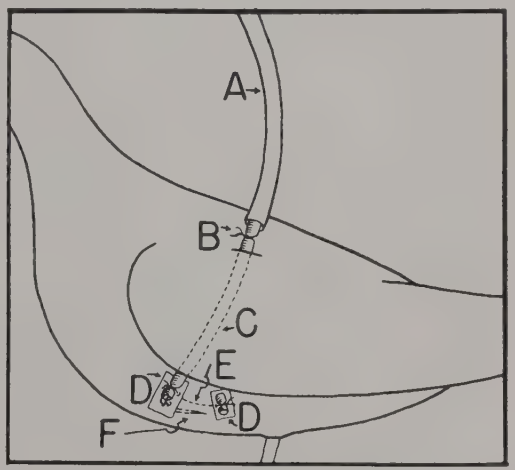

FIG. 1. Method of securing thermocouple for continuous recording of body temperature of mourning doves. A, rubber tubing. B, stitch through scapular region of dorsal feather tract. C, thermocouple leads inclosed in vinyl tubing passing beneath wing. D, crinoline pads. E, thread secured to thermocouple, stitched through pectoral muscle and fastened to a small piece of vinyl tubing. F, thermocouple implanted deep in pectoral muscle.

Pads of light crinoline dusted with sulfanilamide powder prevented injury and post-operative infection at the point of insertion of the thermocouple and at the point of emergence of the thread used for securing the thermocouple. Strain on the point of insertion of the thermocouple was prevented by tying the thermocouple leads to a stitch taken through the interscapular region of the spinal feather tract. Kinking of the leads was prevented by sheathing them in vinyl tubing and rubber tubing (Fig. 1). During the long-term experiments, the birds were housed in 8 x 8 x 14

[1] These studies were aided in part by a contract between the Office of Naval Research, Department of the Navy, and the University of California (NR 160 171).

inch cages of half-inch wire mesh. The thermocouple leads were secured to the roof of the cage with rubber bands which acted as shock absorbers. Unless otherwise specified, food and water were available at all times. The birds appeared to experience no particular discomfort from the implanted thermocouples. They walked about freely, ate, and drank, without ever becoming tangled in the leads. No birds died as a result of surgery and all flew normally when the thermocouples were removed. Before measurements were begun, the birds were allowed to rest overnight after surgery to allow them to recover fully from the effects of anesthesia.

During the experiments the cages were placed in a 24-cubic-foot ventilated cabinet in which the temperature was controlled to within 1° C. Light was supplied by daylight fluorescent lamps. The periods of light and dark were controlled by automatic timing switches. During the tests the completely undisturbed birds could be observed through a small window in the door of the cabinet.

In the short-term experiments, simultaneous measurements were made of deep body temperature, skin temperature beneath the feathers of the breast, and skin temperature on the tarsometatarsus. The deep body temperature was obtained from a round-tipped thermocouple inserted through the cloaca into the large intestine to a depth of approximately 3 centimeters. The leads from this thermocouple were taped to the tail feathers. The skin temperature beneath the feathers of the breast was obtained from a thermocouple held with a small piece of adhesive tape against the skin of the pectoral muscle between the ventral feather tracts. The skin temperature of the tarsometatarsus was measured with a thermocouple held in place by adhesive tape. The experiments were run in the dark in the previously described cabinet. The bird was kept in a narrow cage of wire mesh in which it was free to move forward and backward but was not able to turn around.

The wet- and dry-bulb air temperatures and the temperatures of the various parts of the bird could be registered on the recording potentiometer in any sequence at any time by switches connected to the various thermocouples. At least an hour elapsed between the time a dove was placed in the cabinet and the time when the experiment was begun. This allowed the body temperature to reach a steady state before recording was started.

Water consumption was measured by means of graduated cylinders equipped with "L"-shaped half-inch glass tubes (Fig. 2). The drinking devices were mounted on ringstands with the "L"-tubes extending into the cages. In each experiment one drinking device was used to measure evaporation.

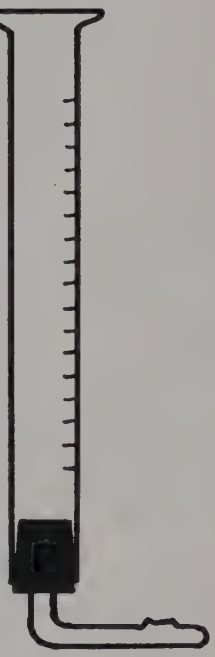

FIG. 2. Drinking device for measuring water consumption of mourning doves. Stopper sealed in the graduated cylinder with beeswax.

BODY TEMPERATURES

Body temperature at moderate air temperatures. Continuous 24-hour records were obtained of the body temperatures of 7 doves kept at 23° C. Like other birds which normally are active only in the daytime, mourning doves show a well-marked diurnal temperature cycle. They are approximately 2 degrees cooler at night than during the day (Fig. 3). The daily temperature cycle is keyed to the daily photoperiod. Under the experimental conditions the lights were turned on abruptly, and as a result the transition of body temperature from the nighttime level to the daytime level was very rapid. The change in body temperature at night after the lights were turned off was less rapid.

The body temperatures of mourning doves are labile. Although the mean daytime body temperature was 41.5° C., the observed daytime temperatures varied between 39.4 and 43.3° C. (Fig. 3). The rapid fluctuations of body temperature result from variations in activity. A sudden burst of activity may cause a rise of as much as 2.2° C. in 4 minutes. There is no regular daily maximum

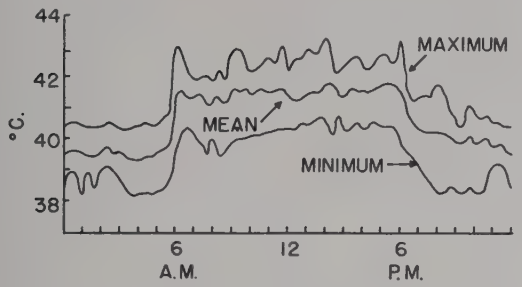

FIG. 3. Summary of the daily temperature cycles of 7 mourning doves kept at an air temperature of 23° C. The maximum and minimum are composite curves obtained by taking the highest and lowest body temperatures at 20 minute intervals from the temperature records of all 7 doves. The mean is based on all 7 records. Light period, 6:00 a.m. to 6:00 p.m.

in body temperature—the occasional peaks are related to brief periods of increased activity. There is, however, a regular daily minimum which occurs in the predawn hours and is associated with the prolonged low level of activity during the night.

Body temperature at low air temperatures. Continuous 24-hour records were obtained of the body temperatures of 3 doves kept at 5° C. These birds maintained their body temperatures at approximately the same levels both day and night as those kept at 23° C. (Fig. 4). One individual slept for two hours during the middle of the day and during this period cooled down to the nighttime level.

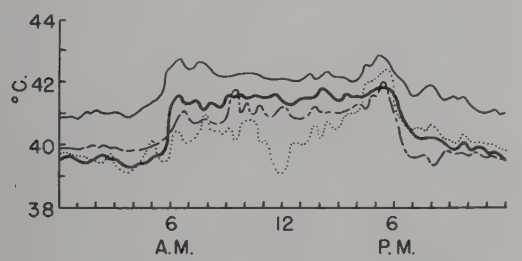

FIG. 4. Daily temperature cycles of 3 mourning doves kept at an air temperature of 5° C. For comparison, the mean temperature cycle of 7 doves kept at 23° C. is shown (heavy line). Light period, 6:00 a.m. to 6:00 p.m.

Body temperature at high air temperatures with water available. Continuous 24-hour records were obtained from 4 doves supplied with drinking water and kept at 39° C. and at a relative humidity of less than 50 per cent (Fig. 5). These birds had temperatures higher than those that doves characteristically maintain in the absence of heat stress. The elevation was most conspicuous at night when the body temperatures were approximately 2° higher than the mean nighttime temperatures for doves kept at 23° C. When exposed to high temperatures during the daytime, the level of body temperature was influenced by even slight changes in activity. If the birds remained quiet, their temperatures stayed essentially at the nighttime level. If they became active, their temperatures rose sharply.

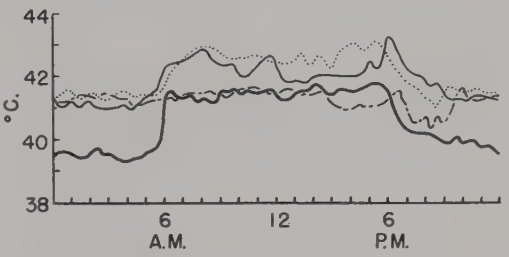

FIG. 5. Daily temperature cycles of 3 mourning doves kept at 39° C. with water available. For comparison, the mean temperature cycle of 7 doves kept at 23° C. is shown (heavy line). Light period, 6:00 a.m. to 6:00 p.m.

The uniformity of the body temperature of doves at night is undoubtedly related to their low level of nocturnal activity. The maximum body temperatures attained by the birds kept at 39° were only slightly higher than the maxima reached by the birds kept at 23°. However, individuals kept at 39° maintained elevated temperatures for longer periods—one bird tolerated a body temperature of essentially 43° for 4 hours without apparent ill effects.

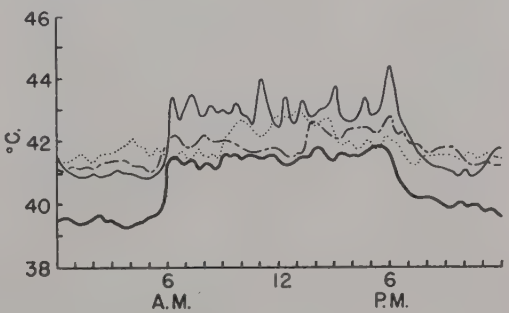

FIG. 6. Daily temperature cycles of 3 mourning doves kept at an air temperature of 39° C. without water. For comparison, the mean temperature cycle of 7 doves kept at 23° C. is shown (heavy line). Light period, 6:00 a.m. to 6:00 p.m.

Body temperature at high air temperatures without water. Continuous 24-hour records were obtained from 3 doves kept without water at 39° and at a relative humidity of less than 50 per cent. These birds, like those kept at 39° with water available, had elevated temperatures at night, but during the day their temperatures were higher and

more variable (Fig. 6). They tolerated their elevated body temperatures without ill effects.

Short-term temperature responses. The short-term effects of rising or falling air temperatures on deep body temperature, skin temperature on the breast, and skin temperature on the leg were observed in 9 doves.

At air temperatures as low as 0° C. the 4 doves tested maintained their deep body temperature at a constant level without shivering or moving about, even when the environment was being cooled at the rate of 1° C. per minute. One dove actually showed a slight elevation of temperature under these conditions (Fig. 7). When the air temperature was decreased rapidly the temperature of the skin on the brest was more variable than the deep body temperature. In the instance illustrated in Figure 7, the skin temperature fell 7° C. in 40 minutes, but in other cases it fell only two or three degrees in a comparable period. A dove kept at 4° C. overnight maintained the temperature of the skin on its breast between 38.8 and 39.4° C. In each of the 5 birds exposed to decreasing air temperatures, the temperature of the skin of the tarsometatarsus fell rapidly (Fig. 7). In two doves maintained overnight at an air temperature of 4° C., the skin of the tarsometatarsus stayed between 3 and 13° C. above the environment and intermittently was subject to sudden elevations of as much as 8° C.

In all cases the birds responded to low air temperatures by fluffing out their feathers, particularly those of the belly. The fluffed feathers of the belly covered all parts of the legs except the toes. One bird, while exposed to 0° C. compressed its feathers thus exposing its legs. As a result the skin temperature of its tarsometatarsus fell about 5° C. in two minutes.

Four experiments were performed to determine the effects of rising air temperature on deep body temperature, skin temperature of the breast, and skin temperature of the tarsometatarsus. All gave similar results (Fig. 8). Short-term exposures to heat had a greater effect on body temperature than did similar exposures to cold.

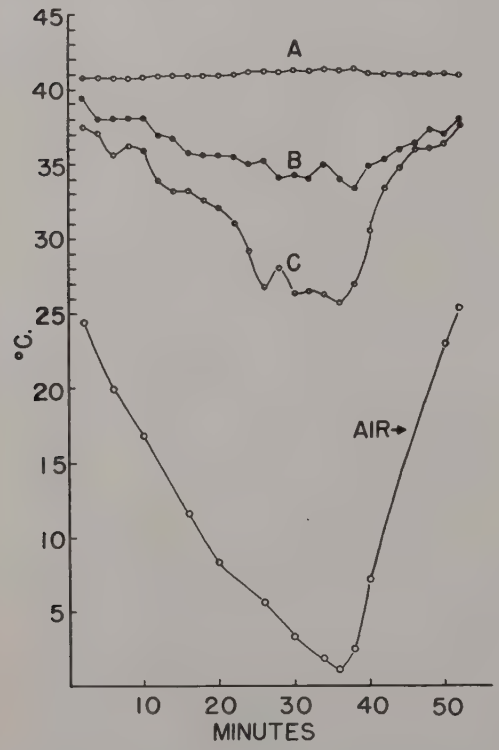

FIG. 7. Effects of decreasing air temperature on temperature of a mourning dove. A, deep body temperature. B, skin temperature beneath feathers of breast. C, skin temperature on tarsometatarsus.

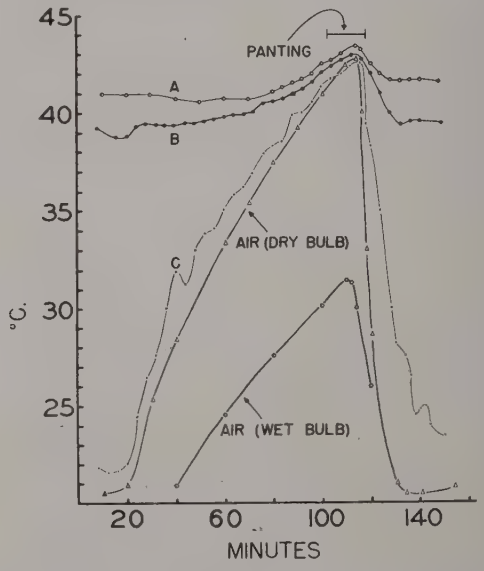

FIG. 8. Effects of increasing air temperature on temperature of a mourning dove. A, deep body temperature. B, skin temperature beneath feathers of breast. C, skin temperature on tarsometatarsus.

At air temperatures up to 36° C. deep body temperature did not change. At air temperatures higher than 36° body temperature rose. The temperature of the skin of the breast was independent of air temperature only up to 30° C. Above this it rose slowly with increasing air temperature. The temperature of the skin of the tarsometatarsus

rose directly with the ambient temperature. When air temperature was reduced rapidly from a high level, the foot and skin temperatures quickly fell to the levels that had been maintained prior to the heat stress. Deep body temperature fell more slowly.

Panting. In all of the short-term experiments, the doves began to pant and flutter their throats when their deep body temperatures reached 42.6° C. Panting and fluttering of the throat continued as long as body temperature remained above this figure. The rate of throat-flutter was in excess of 400 per minute. Panting and throat-flutter ceased in three birds when their body temperatures returned to 42.6° C., and ceased in one bird when its body temperature returned to 42.3° C. Exposures of approximately an hour to high air temperatures caused the animals to hold their wings out from their sides and to compress their feathers. This posture exposes the thinly feathered areas on the sides.

Water Requirements

Water consumption during 24-hour periods was measured for 14 mourning doves kept at 23° and for 5 kept at 39° C. and a relative humidity of 45 to 50 per cent. The birds kept at 39° drank 4 times as much water per day as those kept at 23° C. Birds of neither group showed significant changes in body weight (Table I).

Table I. *Effects of air temperature on water consumption in mourning doves.*

Air temp. in °C.	Number of animals	Mean body weight	Mean amount of water drunk per day		Mean change in body wt. during test (% of original wt.)
			Cc.	% body wt.	
23.....	14	119.7	7.8	6.5	−1.2
39.....	5	120.2	28.8	23.9	+0.6

Doves kept for 24 hours at 39° C. without water lost up to 15 per cent of their initial body weight without apparent ill effects. Within minutes after water was made available, this weight loss was made up by drinking (Table II). Three birds that were maintained without water at 39° C. for 40 to 48 hours continued to drink at a higher-than-normal rate for several hours after water was made available.

The elevated temperatures of doves which were maintained without water at 39° C. (Fig. 6) presumably were a function of dehydration. The effects of water deprivation became progressively more critical as dehydration increased. When doves were allowed to drink water after a period of deprivation, their body temperatures quickly dropped by as much as 1° C. This immediate drop in temperature probably resulted in part from the ingestion of the cool (23° C.) water. However, the continued maintenance of body temperature at the new low level implies that drinking increased the effectiveness of the temperature-regulatory mechanisms.

Discussion

Small birds should be more susceptible to rapid fluctuations in body temperature than large birds, because of their small heat capacity and their relatively large heat production. Even at rest and in the absence of heat stress, the body temperatures of mourning doves fluctuate as much as 0.5° C. in a quarter of an hour. In 7 doves kept at 23° C., the average rise in body temperature in the 20 minutes after the lights were turned on in the morning was 1.7° C. Increased activity frequently caused body temperatures to rise more than 1° C. within 5 minutes. The labile nature of the body temperatures of doves even in the absence of heat stress indicates that for them the result of temperature regulation is not the maintenance of a constant level of body temperature, but the restriction of body temperature to a range of several degrees.

The small heat capacity, relatively large body surface, and relatively high rate of heat production of small birds combine in the presence of heat

Table II. *Dehydration and rehydration in mourning doves kept at an air temperature of 39°C. and a relative humidity of less than 50 per cent. Food available at all times.*

Dove	Orig. wt. (gms.)	Weight after 24 hrs. without water (gms.)	Weight lost in 24 hrs. without water		Weight 4 hrs. after water made available (gms.)	Weight recovery in 4 hrs. with water available		Water drunk after 24 hrs. without water (cc.)			
			Gms.	% orig. body wt.		Gms.	% of wt. lost in preceding 24 hrs.	Minutes after water made available			
								0-10	11-20	21-150	151-210
A.....	109.6	93.3	16.3	14.9	111.6	17.8	109.2	19	2	0	3
B.....	116.0	100.3	15.7	13.5	111.3	11.0	81.5	14	1	1	3
C.....	116.8	109.3	7.5	6.4	125.2	15.9	212.0	20	6	1	0

stress to allow rapid elevations of body temperature which can be counteracted only by effective, rapidly activated mechanisms for heat dissipation; or failing this, tolerance of elevated body temperature. Even when the doves were at rest, high air temperatures caused body temperature to rise, and when they became active, conspicuous fluctuations were the rule. The body temperatures of doves are much more uniform during the night than during the day at all environmental temperatures. Exposure to air temperatures as low as 5° C. and as high as 39° C. failed to eliminate the diurnal temperature cycle. Although the body temperatures of mourning doves vary from 38° to 45° C., our data on panting suggest that their mechanisms for temperature regulation have precise thresholds.

Our observation that panting in the mourning dove commences at a deep body temperature of 42.6° C. is consistent with the data for the domestic pigeon which is also in the subfamily Columbinae. Von Saalfeld (1936) showed that pigeons (presumably *Columba livia*) anesthetized with urethane began to pant at body temperatures between 42 and 43° C., and Randall (1943) found that the threshold for panting in domestic pigeons was between 42.5 and 43.2° C.

In mourning doves, as in domestic pigeons (Udvardy 1951) and various non-sweating mammals (Adolph 1947; Brody 1945) evaporative cooling does not prevent elevation of body temperature when air temperatures approach those of the body (Fig. 8). Thus accessory sites of heat dissipation, for example the comb of the domestic fowl (Yeates *et al.* 1941:121; and others) and the pinna of the domestic dog (Hemingway 1938), may be critical for survival during very hot weather. The legs are the only exposed parts of the mourning dove from which rapid heat transfer might occur. However, our observations suggest that the legs are not sites of rapid heat loss at high air temperatures. At low air temperatures heat loss through the legs is reduced through postural adjustments and probably through vasoconstriction.

Aside from the mouth and the respiratory tract, the principal sites of heat loss at high air temperatures in doves appear to be the thinly feathered sides which are exposed when the birds hold their wings away from the body. As long as air temperature is less than skin temperature, heat transfer to the environment can occur from the skin under the wings. Possibly these areas also serve as important sites of heat loss during flight.

Mourning doves are common throughout the deserts of the southwest. Although they are most abundant near sources of water, their mobility allows them to exploit areas that are many miles from available water (Grinnell, Bryant, and Storer 1918). Apparently it is not necessary for them to drink more than once a day, even in very hot weather. On September 19, 1951, when air temperatures reached 41° C., we made a reconnaissance of the general area around Quail Springs, an isolated water hole in the Mojave desert in San Bernardino County, California. During the daylight hours we observed a number of individual doves in the open desert. Subsequently we kept the water tank under observation for an entire day during which we saw doves only twice, once at 6:00 p.m. (PST) when 13 individuals, after arriving singly in the span of 20 minutes, visited the water together and drank copiously; and again at 5:20 a.m. when two doves visited the tank briefly.

Cowan (1952) reports on the basis of field studies that western mourning doves satisfy their thirst by a single draught. Our laboratory observations show that doves can drink in 10 minutes an amount of water equivalent to over 17% of their body weight (Table II). Apparently this capacity enables them during a single brief visit to water to drink all the water needed to eliminate any water deficits acquired during the preceding 24 or 48 hours. In this respect the mourning dove is comparable to the burro (Dill 1938: 108). Our observations of water consumption by doves at moderate temperatures (23° C.) indicate that they can go 4 or 5 days without water or succulent food and suffer no permanent ill effects. Mourning doves maintain their body weight when exposed to high temperatures when water is available. In this respect they contrast with man, and some domestic animals—dog, cat, rabbit, mouse, and guinea pig (Adolph 1947).

Mourning doves breed throughout the spring and summer, and a single pair may rear as many as six broods in one year (Cowan 1952). Thus during the hottest parts of the year, in addition to using water for evaporative cooling, female mourning doves lose water in egg production, and doves of both sexes lose water in the formation of the crop milk used in feeding the young. Consequently, during the breeding season availability of water is particularly critical.

The mourning doves of southwestern United States leave the more northern and more elevated parts of their range in the winter and move into areas in which temperatures go below 0° C. only briefly. Our data show that mourning doves even at rest easily regulate their body temperatures when exposed for 24 hours to temperatures near freezing. Thus it is probable that low temperatures *per se* rarely present a serious problem to mourning doves in the Southwest.

A number of factors contribute to the success of the mourning dove in meeting the extremes of heat and aridity in the desert. Its capacity to endure elevated body temperature without damage simplifies its over-all problem of heat regulation. Unlike some desert birds it is not confined to the immediate vicinity of water. Its capacity to withstand dehydration, its capacity for sustained and speedy flight, and its capacity to make up large water deficits in a few minutes combine to allow it to range widely over the desert with only periodic visits to water.

Summary

An attempt is made in this paper to correlate laboratory studies on the body temperature and water requirements of mourning doves (*Zenaidura macroura marginella*) with knowledge of their behavior and distribution in the deserts of southwestern United States.

Twenty-four-hour records of body temperatures in doves exposed to environmental temperatures of 5, 23, and 39° C. were obtained by means of thermocouples implanted in the pectoral muscles.

The diurnal temperature cycles of doves kept at 5° C. and 23° C. are essentially the same. The daytime temperatures approximate 41.5° C. The nighttime temperature is about 2° lower. Even in the absence of heat stress, during the daytime mourning dove temperatures varied over a range of several degrees C. When kept at 39° C., doves showed elevated body temperatures, with the relative elevation being greatest at night. When deprived of water and kept at 39° C., body temperatures tended to be higher and more variable than when water was available.

Short-term increases in air temperature caused increases in deep body, skin, and leg temperatures. Short-term decreases in air temperature, however, caused decreases only in skin and leg temperatures. The panting threshold for mourning doves is reached at a body temperature of approximately 42.6° C.

At 39° C. doves drank 4 times as much water as at 23° C. Twenty-four hours at 39° without water caused a 15 per cent loss in body weight. This loss was made up within a few minutes of the time at which water was made available.

The capacity of doves to endure elevated body temperatures and extensive dehydration, combined with their capacity to make up water deficits quickly and their ability to fly long distances, allow them to meet the demands of desert existence.

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USE OF P^{32} IN TRACING SOME INSECT-PLANT RELATIONSHIPS OF THE THISTLE, *CIRSIUM UNDULATUM*[1]

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Introduction

While studying the applications of radioactive substances to ecological research, it was surmised that radioactive substances could be applied in tracing plant and animal relationships. The procedure involved labeling the plant with a radioactive substance and tracing that substance from the various organisms feeding on the plant to predators. The relationship of aphids to plants and of ants to aphids has been known for a long time, but in order to test this idea, it was decided to re-examine the relationships through labeling

[1] This work was accomplished in part with the aid of an A. E. C. predoctoral fellowship.

of plant sap with radioactive phosphorus (P^{32}), tracing the ingested sap through the aphid, the resulting honeydew, the ant, the ant nest, and the ant colony. Such a labeling method, if practical, would provide a new tool for the study of such ecological relationships between plants and animals and introduce a method of research of value not only in basic science but also in applied fields such as that of agricultural losses due to insects. The work of Jenkins and Hassett (1950) dealing with the uses of radioactive substances in entomology stimulated thinking that led to this study. Previous work by Hamilton (1935) indicated that a transference of radioactivity from plant to aphid is possible, as did the work of Rodriguez (1948) who made mites radioactive by feeding them on plants grown in radiophosphorus. Carter (1945) demonstrated the transfer of P^{32} from mealy bugs through oral secretions to pineapple plants.

Methods

A large thistle plant (*Cirsium undulatum* (Nutt.) Spreng.) heavily infested with aphids, (*Anuraphis* sp.[2]) was selected for the experiment. This plant was about 26 inches high and had not begun to bloom although large floral buds were formed. The plant was growing in a fenced enclosure 25 feet in radius. Ants of several species were visiting the aphids. Phosphorus^{32} was introduced into the base of the plant by making a small cut in the side of the plant, hollowing out a small amount of the pith, and then placing one millicurie of phosphorus in 3 cc of distilled water in this hollow with the aid of a long-needled hypodermic syringe.

This method proved highly satisfactory, and the samples of plant tissue taken 24 hours later showed strong radioactivity to be present throughout the plant. Following this introduction, and as soon as the plant was known to be radioactive, collections were begun of all insects that came to the plant. Systematic sample collections were made daily of the ants and aphids in the area and on the plant.

The method of measurement consisted of taking the ants, aphids, and other insects into the laboratory, identifying them, ashing and desiccating numbers of them, and determining the radioactivity of the specimens with a standard G.M. scaler. In addition, systematic checks were made of the surrounding area to locate the nests of the ants that were using the honeydew. Several ant nests were found in the region, and ants of two species of two different genera were found utilizing the honeydews. These two species were *Formica sanguinea puberula* Emery, and *Camponotus novaboracencis* Fitch. The *Camponotus* ants were found on the plant at the beginning of the experiment and a number were collected and counted.

[2] Specimen identified by the Division of Insect Identification of the Bureau of Entomology and Plant Quarantine of the Department of Agriculture.

Results

The *Camponotus* ants disappeared after the fifth day of observation. No nest of this species could be found in the area included in the study, although a region 50 yards in diameter was examined. Occasionally the tiny ant, *Pheidole californica* Mayr, was encountered, but these ants were apparently only occasionally visiting the plant and were gathering the honeydew dropped on the surface of the plant rather than milking the aphids. Counts on these small ants substantiate this observation, since the counts were always less than the amount taken from a single droplet of honeydew. There were two colonies of *Formica sanguinia puberula* in the area. One nest was 25½ feet northwest of the labeled plant and the other was 15½ feet south of the labeled plant. During the study, no members of the colony northwest of the labeled plant were observed to be radioactive. To check this, the entire colony was excavated at the termination of the experiment, and every possible individual captured and its radioactivity counted. In this counting, none of the individuals, including eggs, and pupae, were found to be radioactive above normal background. The ants in the south colony were found to be approximately uniformly radioactive; this was true of eggs, pupae, and adults. The results of this experiment involving two nests of the same species indicate that territoriality in ants may be more sharply drawn than heretofore believed.

Aphid-ant relationships

Observations on the transfer of honeydew from aphid to ant introduced the question as to whether a quantitative relationship could be established on the basis of unit concentration of the radioisotope in the ant and on the transfer from ant to ant. To test this idea, the radioactivity of the honeydews was determined by taking small, measured pieces of absorbent paper, drying them carefully, and then touching the paper to the anus of the aphid after the ant had stroked the back of the aphid, thus soaking the honeydew into the small piece of paper which was then placed in a planchet and counted. The resulting counts ranged from 8 to 105 cpm. with no two counts similar.

Attempts were made to measure the volume of the honeydew droplets with a capillary tube, but it was found to be impossible to cause the aphid to release honeydew without duplication of the stroking action of the ant antennae. The only method

found to be practical was to wait until the ant had stroked and stimulated the aphid to production and then interpose the paper before the ant could remove the honeydew. As has been pointed out previously, the counting of these honeydew-soaked papers indicated a wide range of concentration and a wide range in size of the honeydew droplets. Concentration and size also varied with the size and stage of development of the aphid, so no definite number of honeydew droplets could be assigned to any one ant.

Study of the aphid-ant relationship showed that the aphid at no time concentrated as much radioactivity as did the ants feeding on the honeydews. It would appear that aphids, after reaching a concentration maximum in 72 hours of feeding on the radioactive plant, send the excess material on through in the honeydew, in effect, acting as a "straw" through which the ant receives the radioactive juice from the plant with, at most, little removal of phosphorus.

Ants captured on the plant, where they were actively gathering the honeydew, showed a great deal more radioactivity than those captured within the nest. Those on the plant showed concentrations up to 15,610 cpm. whereas those in the nest in few instances showed more than 800 cpm. The few ants showing high radioactive counts captured in the nest are assumed to be recent returnees from the plant. Only four of these were found when the nest was excavated. This would appear to confirm the idea that food materials gathered outside the nest in a liquid form tend to be distributed rather uniformly throughout the population. Pupae and eggs taken from the excavated nest were also radioactive to approximately the same degree as the adults.

The problem of differential concentration within the aphids as compared with that of the honeydew concentrating ant would indicate that the two insects have different methods of removing excess metabolites. The aphid apparently has a mechanism whereby excess materials coming out of the plant juices can be by-passed and eliminated in the honeydew when the supply necessary to the body has been achieved. The ant, however, appears not to lose this material except through natural defecation and transfer to others. This differential concentration offers a basis for future experiments on the aphids involving the mechanism by which such metabolites are by-passed.

P^{32} concentration in predators compared with that in the commensal

The honeydews tested showed from 8 to 105 cpm. Because of this great variation, the number of honeydews eaten by an ant could not be determined satisfactorily. That is, no distinct unit increases could be ascertained in the ants when they were counted. In contrast to this, were known predators, such as the ladybird beetles (*Coccinella*

TABLE I. *Summary of radioactivity and calculated predation of insects associated with Cirsium*

	Sample Number	Counts per minute	Calculated No. of aphids taken
Spider (*Pellenes* Sp.) (predator)	1	272	2-3
	2	120	1
	3	180	1
	4	267	2
Lady bird beetles (*Coccinella transversoguttata* and *C. novemnctata*) (predators)	1	1,490	6
	2	2,683	11
	3	269	1
	4	1,520	6
	5	883	3
	6	620	2-3
	7	214	1
	8	946	4
	9	189	1
	10	837	3
	11	569	2
	12	931	3-4
	13	1,363	5
	14	1,824	7
Aphid (*Anuraphis* sp.) (phytophagous)	Average of 100 counted after 72 hours.*	250 (Range-212-602)	
Fly larvae (*Eupecdes vclucris*) (predator)	1	2,610	10
	2	3,460	14
	3	1,264	5
	4	3,564	14
	5	2,005	8
(small)	6	238	1
(small)	7	275	1
	8	2,685	10
	9	5,716	23
Beetle (*Scymnus weidri*, Coccinellidae) (predator)	1	962	4
	2	2,245	9
	3	605	2
Wasp (*Diplazon laetatorius*) (Non-feeding predator provisioning for young)	1	38	
	2	30	
Wasp (*Diplazon tibiatorius*) (Non-feeding predator provisioning for young)	1	28	
	2	43	
	3	36	
	4	27	
Ant (*Camponotus novaboracensis*) (Honeydew collector)	1	494	
	2	748	
	3	1,231	
	4	3,638	
	5	1,047	
	6	3,012	
	7	1,590	
	8	2,961	
	9	5,652	
	10	6,250	

*Seventy-two hours after labelling the *Cirsium*, a sample of 1/10 cc of fluid atken from the stem among the aphids contained 65 counts per minute.
†Found dead at base of plant.

	Sample Number	Counts per minute	Calculated No. of aphids taken
Ant (*Formica sanguinea puberula*) (Honeydew collector)	1	6,272	
	2	1,707	
Representative sample of adults taken from *Cirsium*.	3	14,848†	
	4	701	
	5	1,117	
	6	5,771	
	7	533	
	8	4,073	
	9	414	
	10	274	
	11	7	
	12	8	
Random sample of pupae excavated from nest. (Recipients of honeydew)	1	629	
	2	542	
	3	967	
	4	696	
	5	816	
	6	1,091	
	7	865	
	8	789	
	9	621	
	10	717	
Selected sample of adults excavated from nest.	1	847	
	2	580	
	3	640	
	4	696	
	5	745	
	6	5,983	
	7	716	
	8	462	
	9	737	
	10	1,009	
	11	1,143	
	12	835	
Ant (*Pheidole californica*) (Honeydew collector)	1	11	
	2	16	
Honeydews	1	96	
	2	8	
	3	11	
	4	105	
	5	87	
	6	82	
	7	8	
	8	67	
	9	6	
Fly (*Ephydridae*)	1	1,322	
Fly (*Orellia occidentalis*) (Honeydew collector)	1	120	
Fly (*Eupeodes volucris*) (Honeydew collector)	1	322	
	2	605	
	3	27	
	3	29	
Bees (*Halictus* sp.) (Pollen and nectar collectors)	1	10	
	2	171	
	3	14	
	4	122	
Wasps (*Xylocelia* sp.)	1	77	
	2	93	

transversoguttata Feld and *Coccinella novemnotata* Hbst.) captured on the plant among the aphids. The aphids gave counts of 200 to 600 cpm. with an average of 250 cpm. It was noticed that the ladybird beetles and other predators increased their concentrations in multiples of this amount so that ladybird beetles would yield, for example, 1490 cpm. or 2683 cpm., or other similar rough multiples (see table I). This was interpreted to indicate the number of aphids that had been eaten recently.

As an example of the value of the unit predation concept, a group of dipterous larvae were observed among the aphids on the leaves. These larvae could not be accurately identified at the time and they could not be successfully reared out of the pupae collected. It was possible, however, to definitely ascribe predaceous activities to them on the basis of the unit increases in radioactivity (238 cpm. to 5716 cpm.). These counts increased in definite multiples of approximately 250 cpm. as did those of the previously mentioned ladybird beetles.

Further checking of these larvae proved the accuracy of the predations ascribed to them when it was learned that they belonged to an aphid-eating group of two-winged flies (*Eupeodes volucris* D.D., Syrphidae). Similarly, a coccinellid beetle (*Scymnus pullus weidti* Csy.) was also determined to be an efficient predator.

This analysis did not explain the activities of some small wasps (*Diplazon laetatorious F.* and *D. tibiatorius* Thum) that were capturing aphids on the leaves and carrying them away. Upon testing, it was found that the concentrations in them were extremely low and usually did not equal a tenth of the concentration found in a single aphid. It then became apparent that these Hymenoptera were being labeled slightly as they penetrated the body of the aphid in preparation for carrying it to their burrows which they were presumably provisioning with aphids. It would be interesting to know to what extent the resulting larvae feeding upon these aphids became radioactive. These observations do not agree with the statement that *Diplazon laetatorius* feeds on larvae of Syrphids (Heiss 1938). Furthermore, no wasps of that species emerged from the puparia of the Syrphids under observation.

Spiders (*Pellenes* sp., Salticidae) were also captured in the vicinity and these showed a different type of concentration of the radioactive material. They were radioactive in sufficient quantity to indicate that they were preying on the aphids, but they did not have enough to indicate that the aphid had been completely consumed. The counts appeared to indicate that only ½ to ⅔ of the radioactivity of each aphid was being transferred to the spider.

Non-predaceous visitors

Several insects were associated with the plant that were obviously not predators on the aphids. Some of these, such as Diptera, were attracted to the spilled honeydew that was trapped in the tomentose surface of the *Cirsium* plant. Some of these flies (*Orellia occidentalis* Snow, Diptera, Tephritidae and *Eupeodes volucris* D.S., Diptera, Syrphidae) were visiting the plant long before any of the flowers had opened. These were observed to move among the aphids on the leaves and the stems but no actual observation of their taking honeydews was noted. They proved to be radioactive before the flowers opened, thus establishing a relationship that had not been observed before. That is, these flies come to the source of honeydew and take it up directly from the surface of the leaves where it has been spilled by the aphids.

After the flowers had opened, a number of pollinating insects were observed in the vicinity, and some of these were captured and their radioactivity counted. It was found that some small bees (*Halictus* sp., Hymenoptera, Halictidae) and a small wasp (*Xylocelia* sp., Hymenoptera, Sphecidae) contained 10 to 171 cpm. of radioactivity.

Flowers that were tested indicated that the pollen contained considerable radioactivity, possibly because of the large quantities of nucleo-proteins in which the phosphorus would be incorporated. After removing the pollen and stamens, these flowers were centrifuged for 20 minutes at high speed. Although the liquid nectar in the base of the tube was determined by microscopic analysis to be virtually free of pollen, it was also found to be radioactive. Thus, pollinating insects, and nectar-seeking insects, can be traced from source of origin to various other locations by means of radioactive labeling of the plant proper.

Conclusions and Summary

From this study, it is apparent that determination of the phytophagous insect/predator complex and plant pollinator relationships by labeling a plant with radioactivity is a much more accurate ecologic technique than observation alone. This method can be utilized as a refined technique in the verification or rejection of many conjectural concepts in economic entomology. It establishes a method which is simple yet extremely accurate and safe. It is entirely possible that hundreds of investigations can be made this way, each utilizing a different species of plant and thereby revealing the various insects associated with it.

Second, this offers a new method for examining territoriality in insects and possibly it could be applied to the determination of territoriality in vertebrates.

Third, the method offers a clue to the largely unanswered pollination relationships that exist in crop plants as well as in indigenous plants. By this method, the economic importance of various types of insects could be established and the total effective range of the activity and the specificity of various insects could be investigated.

In agriculture, the method offers a possible means of testing the total amounts of tissue or total amounts of plant saps taken by insect pests.

Finally, this method opens up a new field for the autecologist who is concerned with the more intimate relationships between a given species of plant and its insect and vertebrate visitors.

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RELATION BETWEEN CIRCULATION AND PLANKTONIC POPULATIONS IN ESTUARIES[1]

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Introduction

The study of planktonic populations in estuaries is complicated by the continuous movement of the water. The tides move the water back and forth, so that at a given location the population at low tide may be quite different from that present at high tide. In addition to the obvious flood and ebb tidal movements, the water masses have a net motion which results from inequalities of the tidal movements. The seaward drift of the diluted water must be adequate to remove the fresh water constantly added to the estuary from the rivers.

[1] Contribution No. 598 from the Woods Hole Oceanographic Institution.

The landward drift of more saline water must supply enough sea water to maintain the salt balance by bringing into the estuary an amount of salt equal to that entrained with the fresh water. It is obvious that planktonic populations will be distributed throughout the estuary by these water movements.

If the circulation were the only process influencing the size of the population throughout the estuary, the problem would be very simple. For a population originating in the seaward end of the estuary the expected distribution would be directly proportional to the salt content of any water sample. If the population originated at the fresh water end of the estuary its distribution would be proportional to that of the fresh water, *i.e.* inversely proportional to the salt content. These simple relationships are never found because the population grows or dies within the estuary, and frequently the reproduction rate or the death rate is very different in different parts of the estuary.

The rates of reproduction or of death of a planktonic population within the estuary can be derived only when the rate of circulation is taken into account. It is the purpose of this paper to indicate how this may be done, and to illustrate how the circulation may impose minimum requirements for the rate of reproduction of a population if it is to survive within the estuary.

Theoretical Considerations

A basic assumption in the analysis is that the populations considered are distributed at random by the same processes that control the distribution of fresh and salt waters. The distribution of populations which exhibit vertical gradients, by means of vertical migrations for example, may be unpredictable by these methods. High concentrations of the population in the surface, fresher water would result in more rapid dispersion than the average, since this is the route by which the fresh water escapes seaward. High concentrations in the deeper, more saline water, which is the location of the landward counterdrift, would result in a slower dispersion than the average. Since vertical distribution may vary with time, and vertical migrations may be diurnal in character, and thus out of phase with the flood and ebb of the tide, generalizations concerning the distribution of such populations are not attempted in this paper.

The net result of the circulation in each estuary must be to move seaward, across any complete cross section, during each tidal cycle, a volume of fresh water equal to that introduced by the river during the same period of time. It has been shown that, for selected segments of an estuary, an exchange ratio can be defined as the proportion of the water which moves seaward and does not return on a following flood tide. This same proportion of any planktonic population must also be lost downstream. There is, thus, a constant drain on the population, and enough new individuals to balance this drain must be produced if the population is to maintain itself.

Let us first consider the case of an endemic population, by which is meant specifically a population which is maintaining itself within the estuary and is not receiving recruits from upstream or downstream during the tidal cycle. For such a population the standard growth equation and a simplified circulation equation can be combined. The growth equation is:

$$P_t = P_0 e^{kt} \qquad (1)$$

in which P_0 and P_t are the size of the population initially and after time t, and k is the coefficient of reproduction rate.

As a result of the circulation alone, the population remaining after being depleted by a series of tidal cycles is given by:

$$P_m = P_0 (1 - r)^m \qquad (2)$$

in which m is the number of tidal cycles, and r is the exchange ratio, defined as the proportion of the water moving seaward during each tidal cycle, which does not return on the following flood tide (Ketchum 1951).

Expressing time in the growth equation in terms of tidal cycles, the combination then gives:

$$P_m = P_0 (1 - r)^m e^{mk} \qquad (3)$$

If the population remains constant, $P_m = P_0$, and the growth rate required to balance the depletion by circulation can be defined in terms of the exchange ratio, *i.e.*

$$e^{mk} = \frac{1}{(1 - r)^m} \qquad (4)$$

or

$$k = -\ln (1 - r) \qquad (5)$$

This equation thus defines the rate of reproduction necessary to maintain a population in the estuary in spite of continuous depletion by the circulation. Obviously, if the rate of reproduction is greater than this value the population will increase; if less, the population will decrease.

The relative size of a population in a tidal segment of an estuary as a result of various growth rates is given in Figure 1. For this example an exchange ratio of 0.5 has been used. A similar pattern would be obtained for any other exchange ratio, except that the time scale would be changed. The numbers on the chart indicate the size which would be attained by the population if the circulation were not constantly depleting it. If the population did not reproduce at all it would de-

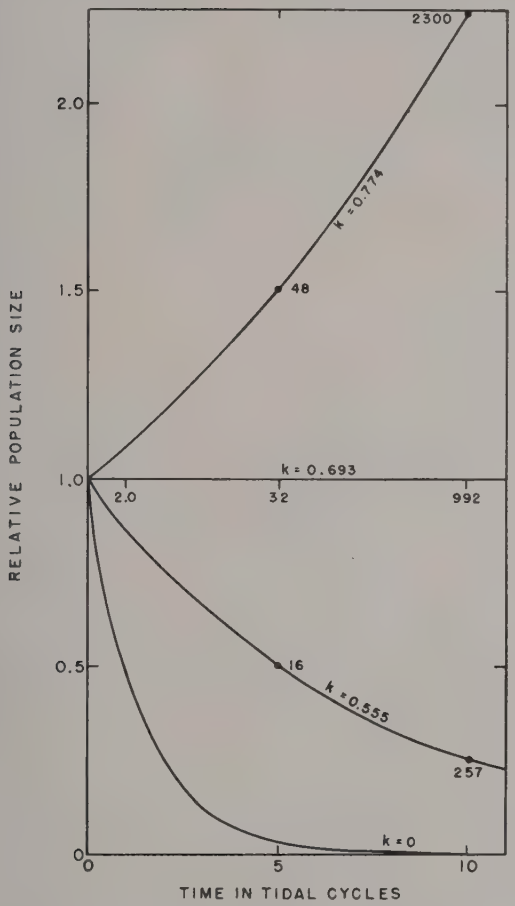

FIG. 1. The effect of the rate of reproduction on the relative size of an endemic population after various times, as tidal cycles, in a segment of an estuary having an exchange ratio of 0.5. The numbers indicate the size the population would have attained if it were not depleted by the circulation.

crease as shown by the lowest curve. This sort of decrease would be expected for a population of larvae released into the segment of the estuary. The horizontal line indicates the population which is just able to maintain itself within the estuary. It will be noted that in this example reproduction must double the population each tidal cycle to balance the removal. During ten tidal cycles reproduction must produce almost a thousand individuals which are lost downstream, although direct observations of the population in the water would indicate no change in population size. The other two lines in this figure indicate the net effect of a reproduction rate greater than, and less than, that required to balance the depletion by the circulation.

It is clear that organisms which can maintain a constant population in some estuaries may be unable to do so in other estuaries where the circulation is more vigorous. For each estuary the rate of reproduction required to maintain a population may be defined in terms of the appropriate exchange ratio, with the results shown in Figure 2. The line drawn in this figure indicates the rate of reproduction required to balance the depletion by the circulation, but does not, of course, indicate what any population will actually do in any estuary. If the growth rate is greater than that required, the population will increase; if less, it will decrease. The average exchange ratios for various estuaries are indicated on this figure.

Moriches Bay, on the south shore of Long Island, has a small exchange ratio and a population should be able to maintain itself with a very low rate of reproduction. In Barnstable Harbor, on the other hand, the tidal exchange is very great, and a population would have to increase rapidly to maintain itself. It is of interest that in the former estuary the population is endemic and characteristic, whereas in the latter the population is strikingly similar to that of the adjacent ocean water outside the limits of the harbor.

In every estuary there must be some region beyond which the organism considered is unable to grow, because of reduced salinity or some other unfavorable condition. The population in this region will not be augmented by new members from upstream, and the foregoing discussion will apply. For all parts of the estuary downstream, however, new members are being introduced into the population from upstream while other members are being carried downstream during each tidal cycle. To take account of both the increment to the population from upstream and loss downstream a different calculation is required. The derivation of the expression for this process has been given by Ketchum, Ayers, and Vaccaro (1952). It is based upon the combination of the equation for the steady-state accumulation of river water in a tidal excursion segment and the growth equation. The former is (Ketchum 1951):

$$Q_n = R \left\{ 1 + (1 - r_n) + (1 - r_n)^2 + (1 - r_n)^3 + \ldots + (1 - r_n)^m \right\} \quad (6)$$

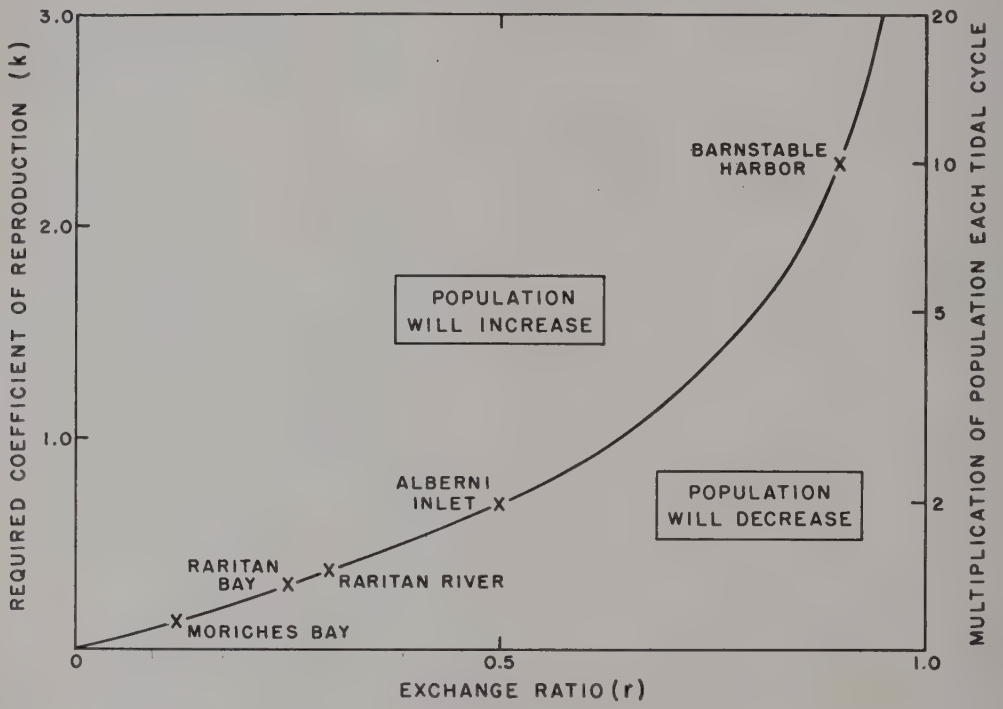

FIG. 2. The coefficient of reproduction required to maintain steady state, endemic populations in estuaries as a function of the exchange ratio.

in which Q_n is the quantity of river water accumulated in the nth tidal excursion segment, and R is the river water introduced to the estuary during a tidal cycle. The combined circulation and growth equation gives:

$$P_n = (P_0)_n \frac{R}{Q_n} \left\{ 1 + (1 - r_n)e^k + (1 - r_n)^2 e^{2k} + (1 - r_n)^3 e^{3k} + \ldots + (1 - r_n)^m e^{mk} \right\} \quad (7)$$

in which $(P_0)_n$ is the increment of population to the nth segment during a tidal cycle, P_n is the steady-state level of population achived as a result of a series of tidal cycles, and the ratio R/Q_n is the exchange ratio, r_n. As the number of tidal cycles becomes large this series approaches:

$$P_n = (P_0)_n r_n \frac{1 - (1 - r_n)^m e^{mk}}{1 - (1 - r_n)e^k} \quad (8)$$

Let us consider what will be the result of such a regime within an estuary. Under these conditions a steady-state population level can be maintained with a variety of rates of reproduction rather than with one alone. For example, if the population did not grow at all within the part of the estuary under consideration the population would nevertheless tend to increase until it approached the size of the population being introduced from upstream, as shown in Figure 3. The rate of reproduction which is necessary to maintain a steady-state endemic population, as discussed above, will theoretically permit the population to increase indefinitely in a location where an increment from upstream is available. Since the reproduction of the population balances the depletion by the circulation, the population will increase by the amount introduced each tidal cycle. To be ecologically more precise, it could be stated that this rate of reproduction would permit the population to increase until crowding or some other factors operated to decrease the reproduction rate.

Any reproduction rate less than that required to maintain an endemic population will produce a steady-state population if increments are also being introduced from upstream. Positive reproduction rates will produce populations greater than the increment from upstream. Even a negative reproduction rate, or in other words an excess of death over reproduction, will permit the attainment of a steady-state population which,

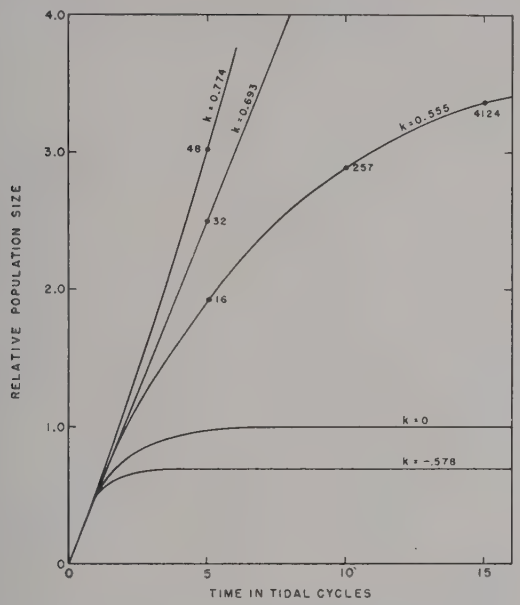

FIG. 3. The effect of the rate of reproduction on the relative size of a population which is being augmented by increments from upstream for various times, as tidal cycles, in a segment of an estuary having an exchange ratio of 0.5. The numbers indicate the size the population would have attained if it were not depleted by the circulation.

however, will always be smaller than the increment from upstream. The steady-state population size under these conditions is given by:

$$P_n = \frac{(P_0)_n r_n}{1 - (1 - r_n)e^k} \qquad (9)$$

This simplification of equation (8) is valid only when e^k is less than $1/(1 - r)$.

It is clear from the foregoing statements that a single simple figure cannot be presented to describe conditions in an estuary where the population is both being augmented from above and decreased by losses seaward. A family of curves is presented in Figure 4 which relate the population size expected after a large number of tidal cycles to the rate of reproduction of populations for estuaries having various exchange ratios. All of the curves cross at a reproduction rate of zero and a relative population size of unity, indicating that the population is the same as that being introduced by the circulation during each tidal cycle. When the reproduction rate is positive, the population developed will be larger in those estuaries with smaller exchange ratios. If, however, the population is dying within the part of the estuary considered, larger populations will be obtained in estuaries having the larger exchange ratios. The reason for this is that the population is present in the estuary for a shorter period of time if the exchange is great, and consequently the population is not so greatly depleted by death.

Reproduction Rates

The foregoing discussion has advanced the thesis that the circulation of the estuary defines the minimum rate of reproduction which will permit the existence of a population in an estuary. It is pertinent to inquire whether populations can be expected to grow at such rates.

For the micro-organisms which reproduce by simple division there is a wealth of information available. Among the bacteria the division rate may be very great and a single cell can, under favorable conditions, produce many thousands of offspring during the course of one tidal cycle. Bacteria can easily replace the depletion resulting from the exchanges if conditions for growth are suitable. Under unfavorable conditions, however, such as are encountered by pollution bacteria in estuaries, the population may fail to grow, or may die at an appreciable rate as a result of the bactericidal action of sea water and predation (Ketchum, Ayers, and Vaccaro 1952). In such cases the circulation has a pronounced effect on distribution.

Some reproduction rates which have been observed with phytoplankton populations are given in Table I. From these rates the relative size of the population after a complete tidal cycle, and the fraction of the population which can be replaced by reproduction during a complete tidal cycle have been computed.[2] This fraction is a direct indication of how vigorous the exchange may be without depleting an endemic population within the estuary. In general it may be said that local phytoplankton populations may be expected to maintain themselves within estuaries where the exchange ratios are about 0.5 or less. Greater exchanges would tend to deplete the population more rapidly than it can reproduce itself.

Most animal populations do not reproduce by simple division, and one may be interested in considering the rate of production of one of the planktonic larval stages, or in the rate of reproduction of the population as a whole. A great deal of basic information is needed before generalizations about the effects of the circulation on various stages of the life cycle of animal populations can be made.

Clarke (1946) and Riley (1947) have analyzed the production of zooplankton populations over Georges Bank. They derive a maximum net production rate of about 5% per day. This is only

[2] This conversion has been made only for the semidiurnal tidal cycle of 12.4 hours.

TABLE I. *Some reproduction rates of Phytoplankton populations.*

Population	Time to double	Coefficient of reproduction rate		Relative population after tidal cycle $\frac{P_m}{P_0}$	Fraction replaced per tidal cycle $\frac{P_m - P_0}{P_m}$
	days	$days^{-1}$	$tides^{-1}$		
Phytoplankton 1					
minimum.....	7.5	0.093	0.047	1.05	0.048
maximum.....	0.67	1.03	0.53	1.70	0.412
mean.....	1.38	0.50	0.26	1.30	0.231
Phytoplankton 2					
minimum.....	1.50	0.46	0.24	1.27	0.213
maximum.....	0.75	0.92	0.48	1.62	0.383
mean.....	1.12	0.62	0.32	1.38	0.275
Cultures					
Biddulphia 3....	0.42	1.65	0.86	2.36	0.576
Coscinodiscus 4..	0.605	1.14	0.59	1.81	0.447
Nitzschia 5.....	0.58	1.19	0.62	1.86	0.462

[1] Riley *et al.* 1949; 2. Harvey *et al.* 1935; 3. Gran 1927; 4. Jenkin 1937; 5. Ketchum & Redfield 1938.

about half as large as the minimum value given in Table I for phytoplankton populations.

Johnson and Olson (1948) have studied the reproduction of *Tisbe furcata,* a marine harpacticoid copepod. On the average, broods consisting of 57 eggs were produced at intervals of three days. In their experiments there was 80% survival. It can be concluded that two individuals of *Tisbe furcata* can produce 46 viable eggs every three days during the breeding season. The coefficient of the "rate of production" of eggs calculated from these values is 0.522 per tidal cycle, and the fraction of eggs replaced each tidal cycle is 0.408. This is comparable to the rate of reproduction of phytoplankton populations. Johnson and Olson found that the brood of *T. furcata,* however, required between 15 and 31 days to reach maturity. The coefficient of the rate of reproduction of the population as a whole is only 0.106 per tidal cycle for a generation time of 15 days, or about half of that rate for a 31 day period. Thus five to ten per cent of the population can be replaced each tidal cycle.

These estimates of the rate of reproduction of animal populations are admittedly sketchy, but they do indicate, on the whole, that such populations reproduce more slowly than the phytoplankton and are thus less capable of maintaining a unique, endemic population in the upper reaches of the estuary. The planktonic larvae may, however, exhibit vertical migration which could greatly modify their distribution and the effects of the circulation. It would be easy, for example, to postulate that the larvae have a tendency to migrate downwards away from the light and into the more saline water. This would place them in the counterdrift and transport them up the estuary. Such a migration would clearly lead to a higher concentration of the larvae than is calculated from the exchanges of river water. Altogether too little is known about the physiology and rate of production of various stages of the larvae and rate of reproduction of the population as a whole to permit any definite conclusions concerning the importance of the circulation in their life cycle.

Application to Natural Conditions

From the foregoing theoretical considerations it appears that different sorts of populations may be expected in natural estuaries solely as a result of the vigor of the circulation. A few examples may serve to clarify the general application.

An endemic phytoplankton population, consisting of small chlorophytes, develops year after year in Moriches Bay, Long Island, New York (Fig. 5). During the summer months these algae are the predominant members of the phytoplankton population within the bay, though they are rare or absent in nearby waters. The bay is heavily fertilized by drainage from duck farms around the banks of the tributary rivers.

The circulation is slow, and only about 12% of the volume of water present in any tidal excursion segment is exchanged during a tidal cycle. For the bay as a whole the rate of exchange is only about a tenth of this value.

Ryther (1954) has shown by physiological experiments on pure cultures of these algae that they are uniquely suited to grow under the conditions found in Moriches Bay. They are able to grow in nearly fresh water, and optimum growth was obtained in salinities indicative of about 50% sea water. The temperature of the bay water is at or near the optimum (25° C.) for their growth most of the summer. The proportion of phosphorus to nitrogen in the duck farm wastes is close to the optimum ratio for these species.

This is clearly a case of rapid multiplication of a population which is uniquely adjusted to the ecological conditions which exist in the upper, less saline part of the estuary. The slow rate of the circulation permits the accumulation of a large population which is thus placed in a favorable competitive position and maintains superiority in numbers over large areas.

The effect of a rapid circulation on the dispersal of planktonic larvae may be inferred from investigations which have been made in Barnstable Harbor, Cape Cod, Mass. (Fig. 6). As shown by Ayers (unpub.) the exchange ratio for each tidal excursion segment is about 0.9, and for the harbor as a whole the rate of exchange is about one third of this value. The brackish-water planktonic

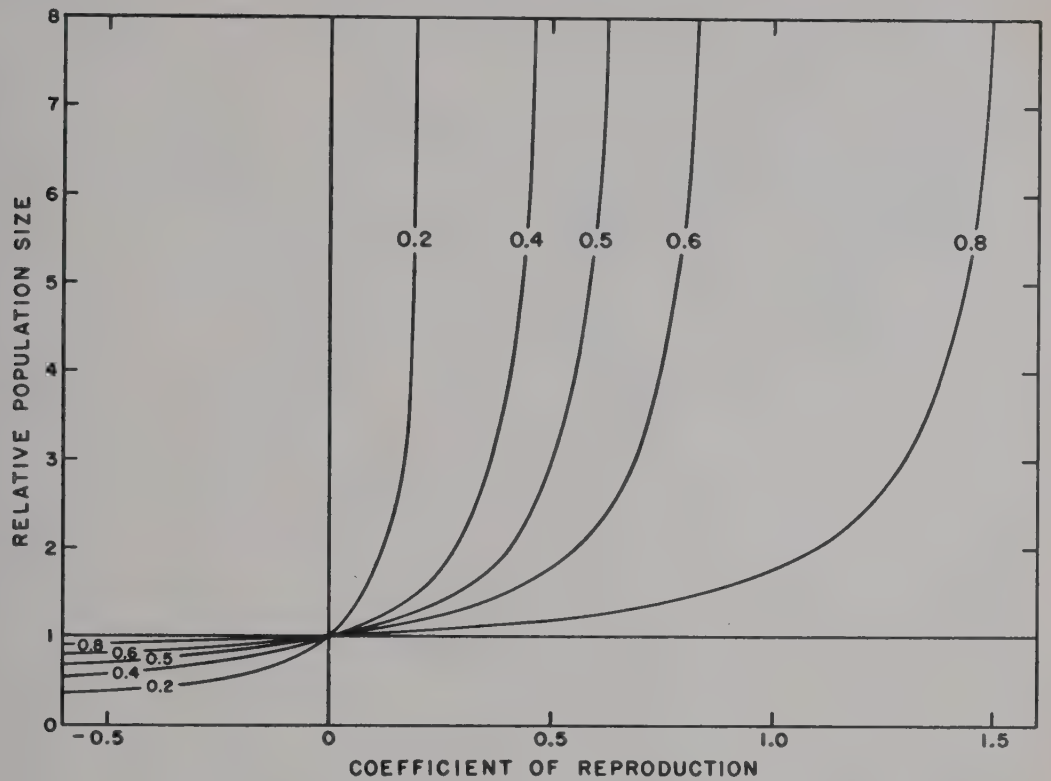

FIG. 4. The relationship between the steady-state size of a population and the coefficient of reproduction for estuaries characterized by various exchange ratios.

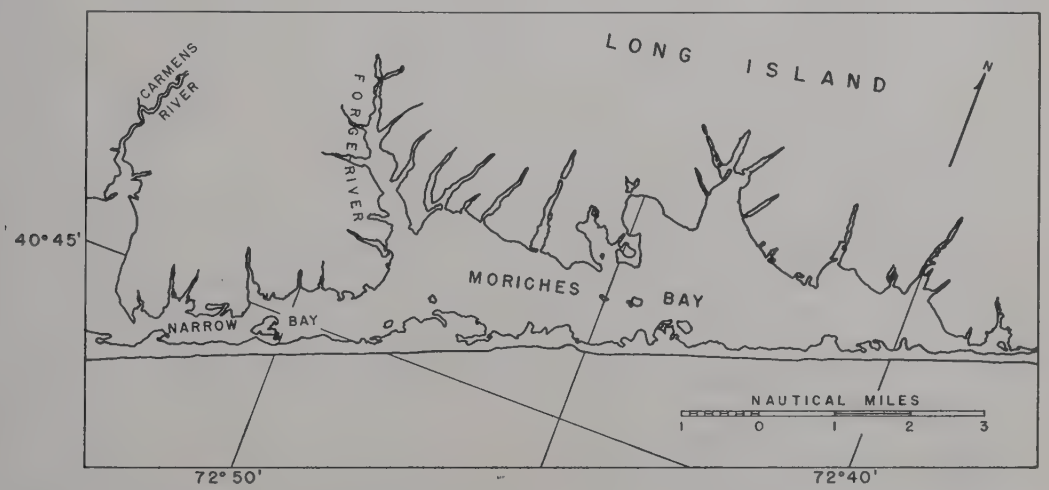

FIG. 5. Moriches Bay on the South Shore of Long Island, New York. The mean tidal range is about 0.4 feet and the average exchange ratio is about 0.12.

forms, therefore have very little opportunity to establish dominance, since they would have to multiply at enormous rates in order to maintain the population. It is not surprising, therefore, that in this location the planktonic population is similar to that of the adjacent ocean waters.

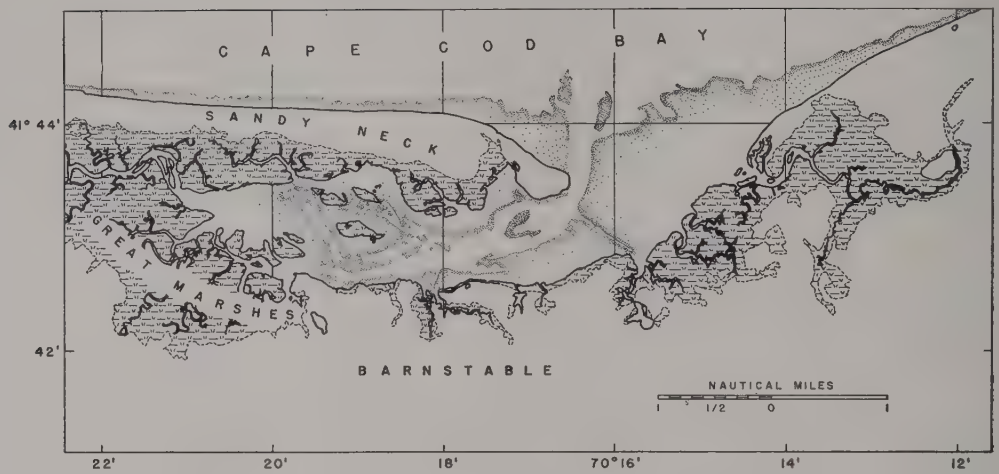

FIG. 6. Barnstable Harbor on the North Shore of Cape Cod, Mass. The mean tidal range is eleven feet, and the average exchange ratio is 0.9.

One of the interesting problems in Barnstable Harbor is that the clam population has decreased to negligible proportions and, as shown by Turner (1949, 1950), efforts to re-establish it have been largely unproductive. According to Belding (1930) a pair of two and one half inch clams can produce about three million larvae, which have a pelagic life of about fourteen days or twenty-eight tidal cycles. From the average exchange ratio of Barnstable Harbor as a whole (0.30) it can be calculated that, as a result of circulation alone, neglecting larval mortality, about 150 spat would be the most which could remain for each pair of clams. Ayers (unpub.) has concluded that mortality between spatfall and maturity alone would leave less than one mature clam annually to replace the population, and considering the possible decimation of larvae by predation and mortality it is not surprising that only rarely indeed is a substantial set obtained.

The distribution of coliform bacteria in the Raritan River estuary is an example of the changes in a population which is both augmented and depleted by the circulation, while being subject to biological changes. In this case the population is introduced at the freshwater end of the estuary at a high level and a nearly constant rate by the sewage effluents of the city of New Brunswick and other municipalities upstream. Because of the bactericidal effect of sea water, the population is dying off as the circulation carries it downstream. The total population decreases by about 100,000 cells/ml. over a ten mile length of the estuary. We found that by taking account of the circulation, of the rate of bactericidal action of sea water, which was measured under laboratory conditions independently, and of the predation resulting from the zooplankton population in the river, we could account for more than 99% of the observed decrease (Ketchum, Ayers, Vaccaro 1952). A correct interpretation of the observed distribution could be obtained only when both the biological processes and the circulation were taken into account.

The final example is drawn from the unpublished work of Barlow (1952) who has studied the zooplankton population of a small estuary, Great Pond, near Woods Hole, Mass. (Fig. 7). Barlow observed that *Acartia tonsa* was apparently endemic in the estuary during the early summer, since maximum numbers of both nauplii and copepodid larvae were found near the head of the main pond where the salinity was about 10-20 parts per thousand. These populations were maintained at high concentrations for weeks in spite of the continuous depletion by the circulation.

The rate of production of these larvae was calculated from the natural distribution by equation 8, and was also determined from experiments in which samples of the water were isolated from the circulation in several 5-gallon jugs which were re-suspended in the estuary. Throughout most of the estuary the rates of production of both nauplii and copepodid larvae as determined by the two independent methods were in close agreement. Both sets of data showed a decrease in the rate of production of larvae with increasing salinity. In the part of the estuary where the salinity was about 10 parts per thousand the production rates indicated that the population of larvae could dou-

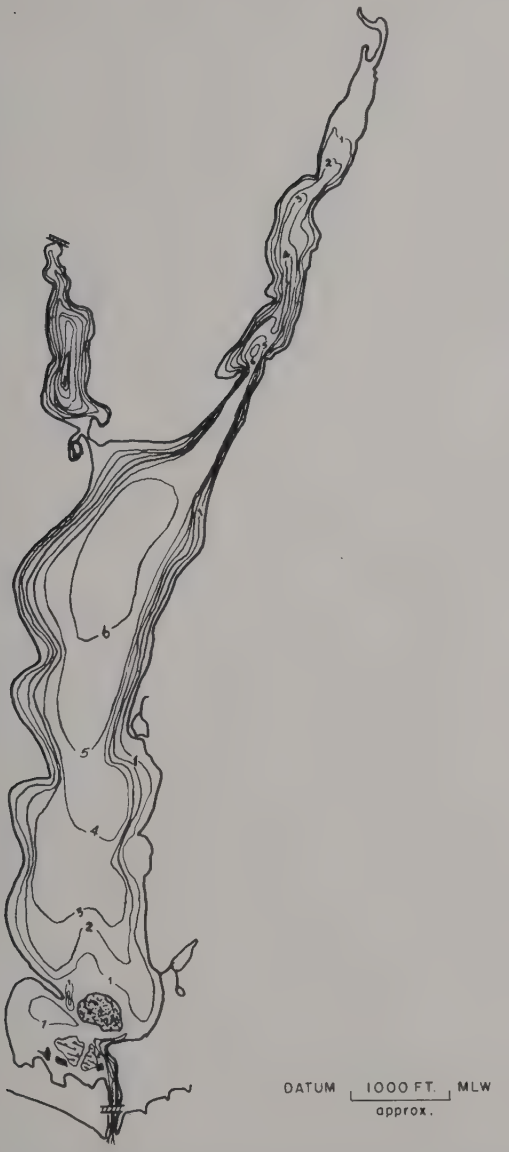

FIG. 7. Great Pond near Falmouth, Mass. The depth contours are shown in feet at mean low water. The mean range of tide is 1.5 feet, and the average exchange ratio is 0.30.

ble in less than a day. This rate of production was necessary to maintain the high population level observed in this region. Near the mouth of the estuary, where salinities were 30 parts per thousand, the larvae had negative production rates which would reduce the population to about a half of its original value in slightly less than one day. In this region the low population was maintained by augmentation from upstream. In the freshest part of the estuary the rate of production obtained in the jug experiments was too low to account for the observed distribution—a discrepancy which Barlow attributes to the recruitment to the population from the deeper water downstream.

The larvae are, of course, only stages in the development of *Acartia tonsa*. The rates of production depend on the rate of production of eggs by the adult and the rate of their development. The negative values in the saltier parts of the estuary are not necessarily indicative of mortality, since similar results could be obtained because of the metamorphosis of the nauplius to the copepodid and of the copepodid to the adult. The importance of these observations is that Barlow has shown that production rates derived from observed distributions in an environment complicated by an active circulation of water are comparable to the rates obtained in a similar environment isolated from the circulation.

SUMMARY

1. The rate at which a planktonic population must reproduce in order to maintain itself in an estuary is determined by the vigor of the circulation. The reproduction rate required for an endemic population is defined in terms of an exchange ratio determined as the proportion of water escaping seaward each tidal cycle.

2. If a population is augmented from upstream as well as depleted by the circulation, a steady-state population will be achieved at a level determined by the rate of reproduction and the rate of the circulation. A method for determining the size of the population expected under various conditions is presented.

3. Examples of the application of these calculations in various estuaries are presented for a bacterial population, a phytoplankton population, the planktonic larvae of a sedentary population, and larvae of a zooplankton population.

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EFFECTS OF MODERATE GRAZING ON THE COMPOSITION AND PLANT PRODUCTION OF A NATIVE TALL-GRASS PRAIRIE IN CENTRAL OKLAHOMA[1]

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The composition of the tall-grass prairie in Oklahoma has received some attention from investigators. Bruner (1931) described the true prairie of Oklahoma, listing *Andropogon scoparius,*[2] *A. gerardi, Bouteloua curtipendula, Agropyron smithii,* and *Sporobolus asper* as dominants. Duck and Fletcher (1945) reported that the natural vegetation of the tall-grass prairie consisted of a mixture of such species as *Andropogon gerardi, A. scoparius, Sorghastrum nutans, Panicum virgatum,* and *Andropogon saccharoides.* Smith (1940) listed *Andropogon scoparius* and *Bouteloua curtipendula* as the dominant grasses in the prairies of central Oklahoma and designated this region as a part of the mixed-grass association. Nease (1948) described the tall-grass prairie of south central Oklahoma and listed four dominants: *Andropogon scoparius, A. hallii, Panicum virgatum,* and *Sorghastrum nutans.* Perhaps the first quantitative work on the composition of the true prairie in the state was that of Rice (1952) in south central Oklahoma. On the basis of cover and frequency he found the dominant grasses, in order of decreasing importance, to be *Sorghastrum nutans, Panicum virgatum, and Andropogon gerardi.*

The purpose of the present investigation was to secure information on grassland dominants and on plant production of a small sample of virgin prairie and a moderately grazed pasture in central Oklahoma. The investigation was initiated in the autumn of 1949 and was continued throughout the entire growing season of 1950.

The writer is indebted to many persons for assistance in the field work and in the preparation of the manuscript. He especially wishes to thank Dr. Wm. T. Penfound and Dr. E. L. Rice under whose joint direction the work was done.

LOCATION AND DESCRIPTION OF STUDY PLOTS

The two plots are located within a few hundred yards of one another on gentle, northeast facing slopes. They are a part of the University of Oklahoma Grasslands Investigation Plots located approximately eight miles southwest of Norman, along State Highway 9 in McClain County, Oklahoma.

The virgin prairie was represented by an area of approximately five acres which has not been burned or grazed in the past twenty-five years. The history of the plot prior to 1926 is not known, but it seems unlikely that it was ever greatly disturbed. Although mowed for hay in 1940 or 1941,

[1] Based on a thesis submitted to the Graduate College of the University of Oklahoma. This paper is one of a series on the University of Oklahoma Grasslands Investigation Plots on land provided by Mr. Neil R. Johnson.

[2] Nomenclature of the grasses is according to Hitchcock and Chase (1950); that of the other species follows Fernald (1950).

it has not been disturbed by man since that time. This plot represents the true tall-grass prairie which at one time extended throughout this area (Bruner 1931). An area comparable in size to the virgin prairie plot was designated as a study area in a grazed pasture of approximately one thousand acres. This plot was located in an area far removed from the water supply and had not been visited by the cattle as often as other portions of the pasture. At times, grazing has been as high as one head per four acres, while at other times when fewer cattle have been in the pasture, the grass was mowed for hay. The study plot was last mowed for hay in the fall of 1948. Grazing during the period of study was only moderate.

Methods

The vegetation of the areas was analyzed by means of 25 one-tenth square meter quadrats on each plot at each of three different times during the growing season of 1950: May 16 to 21; July 24 to 30; October 20 to 30. The quadrats were spaced at intervals of ten paces along predetermined lines of study. The species present in each quadrat were noted and the living areal (foliage) cover of each species was estimated to the nearest whole per cent of the total area of the quadrat. From these data, frequency percentages and average cover percentages for each species were calculated. After the quadrat analysis was completed in each plot, a survey was made of the area and a list was made of all species found that were not included in the analysis. Whenever any doubt existed as to the correct identification of a plant, it was collected for subsequent identification. The collected plants are on file in the Bebb Herbarium of the University of Oklahoma.

In the analysis of the vegetation, two copper squares representing one and five per cent of the total area enclosed by the quadrat were used as aids in estimating cover. Malmsten (1930) suggested that, with practice, errors in ocular estimations of density and cover should be less than 10 per cent of the estimated values. In the present study, three trained investigators, working independently, were in remarkable agreement and their estimations were within the error suggested by Malmsten. A series of quadrats was analyzed in each of the plots late in the fall of 1949 as preliminary to the analyses of the next growing season. Frequency precentages of the unimportant species (importance being determined by percentage cover) were found to be much too high in the virgin prairie when quadrats as large as 0.25 sq. m. were used. When quadrats of 0.1 sq. m. were used, there was close agreement between frequency and cover data. It was also more difficult to estimate cover percentages with the larger quadrat size. For these reasons, the smaller (0.1 sq. m.) size was selected.

In the present study, 25 0.1 sq. m. quadrats were considered sufficient to determine the dominant species of a given area. In view of the fact that three seasonal analyses were contemplated, it was felt that each analysis would serve as a check on each previous sampling. As it developed later, the dominant species, and the order of dominants, were similar in a given plot throughout the spring, summer and autumn samplings. The similarity of dominants in the seasonal samplings indicated that 25 quadrats were ample for the purposes of the investigation.

After the cover had been determined for each species in a quadrat, all the vegetation was clipped at the ground level. Inasmuch as a new series of quadrats was selected for each period of study, none of the areas previously clipped were clipped a second time. The clipped material, as well as the litter and debris, was placed in a paper sack and taken to the laboratory. Oven-dry weights (85°-90° C. for 72 hours) were then determined separately for both the living and the dead material. No attempt was made to separate the living material of the various species since it was thought that the results obtained would not justify the time required.

One of the principal purposes of the quadrat studies was to determine the dominant species in the plots. Many investigators have used basal cover in determining dominance (Albertson 1937, 1938, Hopkins *et al.* 1941, Tolstead 1941, Weaver and Bruner 1948, and many others). On the other hand, some workers (Aikman 1930, Bonck and Penfound 1945, Dyksterhuis 1946, Penfound 1948, Rice 1952, Smith 1940) have used areal cover. Frequency and areal cover have been used in this investigation. Areal cover has been emphasized because it is believed that this type of measurement gives the best relationship between the various species of a grassland community. Bauer (1943) stressed the importance of cover by stating that, "it is coverage rather than numbers of plants or frequency of occurrence or other quantitative concepts used in the analysis of vegetation that determines dominance and gives character to a community. . . . Because of these things coverage data may be thought of as more valuable and significant than other data intended to express the quantitative relations among species."

Soil samples for the determination of soil moisture, organic carbon, and hydrogen-ion concentration (pH) were obtained from two levels of the soil—the first six inches and the third six inches (12 to 18 inches). Six samples were taken from

each level in each of the plots at each sampling period.

Soil moisture, organic carbon (Walkley and Black method), and pH were determined by the methods outlined by Piper (1944). A Beckman pH meter, Model H2, was used in measuring the pH of the soil samples. Organic carbon and pH were determined from portions of the same sample.

Soil samples for the determination of the volume-weights were collected in the following manner: A small hole approximately two inches in diameter and three inches deep was dug with a trowel and all of the excavated material was placed in a small sack to be taken to the laboratory for oven-dry weight determinations. The volume of the hole was then determined by pouring Ottawa gravel into it from a graduated cylinder and noting the volume used. The graduated cylinder was filled in the same manner for each determination, care being taken not to tap the cylinder and pack the gravel. After the oven-dry weights of the soil samples were determined, the volume-weight was calculated by dividing the oven-dry weight in grams by the volume of the soil in cc.

Designation of Dominants

Is is evident that the designation of dominant species in any given community is an arbitrary one. In this paper, the term "dominant" has been applied to those species which possessed a cover of 10 per cent or more of the total living cover for the three sampling periods. Frequency percentages, although not reported in this paper, were calculated and used as one criterion for determining dominance. In general, an average frequency percentage of 50 or more was considered the minimum for designating a plant as a dominant.

Virgin Prairie

From the quadrat analysis of the virgin prairie plot, it is evident that there were three grasses that exhibited relatively high living cover (Table I). Each of these species possessed an average cover for the three sampling periods of 10 or more per cent of the average living cover (living cover per species divided by the total living cover). *Andropogon scoparius, Panicum virgatum,* and *Sorghastrum nutans* should be designated as co-dominants. Perhaps *Andropogon gerardi* also should be included in a list of the dominants since the cover of this species was not significantly different from that of *Sorghastrum nutans* in the spring and summer samplings. *Leptoloma cognatum* and *Aster ericoides* were the important secondary species. The dominants as well as the secondary species in the virgin prairie plot are typical perennial prairie plants that, with the exception of *Leptoloma cognatum,* occur in the tall-grass prairie at least as far north as South Dakota and Minnesota (Weaver and Fitzpatrick 1934).

In general, as cover increased in the virgin prairie plot, the oven-dry weight of the living material also increased (Tables I and II). Although significant positive correlations were found in the spring and summer between the cover percentages and the oven-dry weights of a series of individual quadrats, there was no positive correlation found in the fall sampling. The need for a system of areal cover measurement which includes a height factor is suggested.

Soil moisture data indicate that adequate soil moisture was available in the virgin prairie in both levels of the soil throughout the major portion of the growing season (Table III). The pH of the two levels of the soil was slightly on the acid side with no change with depth being evident (Table IV). The organic carbon values showed no statistical differences between spring and fall samplings. There was, however, a decrease in organic carbon with depth (Table V). Volume-weight measurements varied little throughout the year (Table VI).

Table I. *Cover percentages of principal species in the virgin prairie and grazed pasture for the 1950 growing season (with standard errors)*

Species	Virgin prairie			Grazed pasture		
	Spring	Summer	Autumn	Spring	Summer	Autumn
Panicum virgatum	2.3±0.5	8.5±1.3	5.0±0.7	1.4±0.4	1.6±0.4*	0.4±0.2*
Andropogon scoparius	3.2±0.7	4.4±0.9	5.5±0.7	18.1±2.2*	22.9±2.3*	14.0±1.7*
Sorghastrum nutans	3.6±0.9	5.4±0.9	4.0±0.6	4.2±0.8	5.8±1.2	3.9±0.7
Andropogon gerardi	1.8±1.0	5.8±1.8	1.7±0.5	3.4±1.2	2.1±0.7	1.0±0.3
Lepioloma cognatum	0.3±0.2	2.3±1.2	3.0±1.0	0.3±0.2	4.3±0.8	1.4±0.4
Aster ericoides	1.4±0.4	2.8±0.4	0.5±0.2	0.9±0.4	2.2±0.4	0.6±0.2
Average living cover (all species)	19.3±2.4	41.4±2.8	24.0±1.2	34.6±2.7*	56.5±2.1*	26.3±1.4

*Significantly different (0.01 level) from the virgin prairie.

TABLE II. *Oven-dry weights of living and dead material in the virgin prairie and grazed pasture expressed as pounds per acre (with standard errors)*

	Virgin prarie			Grazed pasture		
	Spring	Summer	Fall	Spring	Summer	Fall
Living	1,177±161	2,872±214	2,471±401	1,481±80	3,684±294*	2,205±205
Dead	10,882±607	8,144±526	9,544±437	5,342±535†	4,496±437†	8,831±767

*Significantly different (0.05 level) from virgin prairie.
†Significantly different (0.01 level) from virgin prairie.

TABLE III. *Soil moisture in the two plots expressed as per cent of oven-dry weight of soil*

Date	0-6 Inches		12-18 Inches	
	Prairie	Pasture	Prairie	Pasture
January 1, 1950	19.0	19.2	17.8	17.6
February 4	17.8	18.0	17.8	19.0
February 28	21.2	21.4	18.2	19.7
April 1	15.5	15.2	17.6	20.0
May 1	17.0	14.6	17.6	19.5
June 1	24.8	20.8	19.8	20.8
June 27	15.1	14.0	16.4	17.6
August 14	15.5	13.0	18.0	18.9
August 31	17.3	15.4	17.7	17.1
September 6	13.8	11.6	....	....
November 2	12.2	10.1	15.4	15.2

TABLE IV. *A comparison of the pH of two levels of the soil in the two plots*

Plots	(4-10-50) Mean*	(4-10-50) Range	(11-14-50) Mean	(11-14-50) Range
0-6 inches				
Prairie	6.3	(6.1 - 6.6)	6.6	(6.4 - 6.8)
Pasture	5.8	(5.8 - 5.9)	6.6	(6.5 - 6.8)
12-18 inches				
Prairie	6.5	(6.4 - 6.6)	6.6	(6.5 - 6.7)
Pasture	5.7	(5.6 - 5.8)	6.7	(6.6 - 6.9)

*The pH values were converted to actual hydrogen-ion concentrations before they were averaged.

TABLE V. *Walkley and Black organic carbon values† (with standard errors) expressed as per cent of air-dry weight of soil*

Plots	(4-10-50)	(11-14-50)
0-6 inches		
Prairie	1.14±.06*	0.98±.03*
Pasture	1.37±.02	1.38±.03
12-18 inches		
Prairie	0.59±.05	0.47±.03*
Pasture	0.64±.03	0.64±.03

†For approximate organic matter values, multiply by 2.15.
*Significantly different from those of the pasture (0.01 level).

TABLE VI. *Volume-weight measurements in first three inches of soil (with standard errors)*

Plots	(2-18-50)	(8-14-50)	(9-20-50)
Prairie	0.8±.04	0.9±.04	0.9±.04
Pasture	1.1±.03	1.2±.05	1.2±.02

GRAZED PASTURE

The major dominant of the grazed pasture, as indicated by both cover and frequency, was *Andropogon scoparius* (Table I). *Sorghastrum nutans* was the only other true prairie grass which occupied sufficient area in the grazed pasture to be considered a dominant. In general, *Panicum virgatum* and *Andropogon gerardi* exhibited much lower cover percentages than in the virgin prairie. The frequency percentages of these two species were also considerably lower. It is believed that they must be considered secondary species.

Total living cover was greater in the grazed pasture than in the virgin prairie at all times (Table I). The total oven-dry weight of living material was significantly greater in the grazed pasture than in the virgin prairie at the time of the spring and summer samplings (Table II). Although the amount in the fall sampling was somewhat less than in the virgin prairie, the difference between the two plots was not statistically significant. It is believed that the reduction in the amount of living material can be attributed to grazing. The amount of dead material was lower in the grazed pasture than in the virgin prairie (Table II). Much of the dead material was in the form of clumps of standing *Andropogon scoparius*.

The number of species encountered in the grazed pasture (64) was considerably greater than in the virgin prairie (36). The larger number of species in the grazed pasture can be attributed directly to the increase in habitat types caused by grazing. Although the pasture was only moderately grazed, grazing was uneven throughout the area. Most of the clumps of *Andropogon scoparius* were left untouched whereas patches between them were grazed close to the ground thereby allowing some of the shorter grasses and forbs to become established. Many of the grasses and forbs found in the grazed pasture are indicators of disturbance. A list of these includes

TABLE VII. *Seasonal distribution and relative importance of all species present in the two plots. (Letters a, b, and c represent spring, summer, and fall, respectively. Capital letters (A, B, C) indicate species with an average cover percentage of 1.0 or more)*

Species	Virgin Prairie	Grazed Pasture
Achillea lanulosa Nutt	a.c	a..
Ambrosia psilostachya DC	abc	abc
Amorpha canescens Pursh	Abc	abc
Andropogon gerardi Vitman	ABC	ABC
A. saccharoides Swartz	...	abc
A. scoparius Michx	ABC	ABC
Anemone caroliniana Walt	a..	a.c
Apocynum cannabinum L	.b.	...
Aristida oligantha Michx	...	.bc
A. purpurascens Poir	.bc	...
Artemisia gnaphalodes Nutt	aBc	...
Aster ericoides L	ABC	aBC
Astragalus caryocarpus Ker	...	ab.
Baptisia minor Lehm	...	a..
Bouteloua curtipendula (Michx.) Torr	abC	aBC
B. gracilis (HBK) Lag	abc	abc
B. hirsuta Lag	...	abc
Bromus catharticus Vahl	...	a.
B. commutatus Schrad	...	a.c
Buchloë dactyloides (Nutt.) Engelm	...	abc
Callirhoë involucrata (T. & G.) Gray	abc	abc
Carex muhlenbergii Schkuhr	...	ab
Cassia fasciculata Michx	abc	...
Chaerophyllum texanum C. & R	...	a..
Chloris verticillata Nutt	...	aBC
Cyperus (sterile)	...	..c
Desmodium sessilifolium (Torr.) T. & G.	a..	...
Eragrostis sessilispica Buckl	...	.b.
E. spectabilis (Pursh) Steud	.bc	.bc
Erigeron canadensis L	abc	...
E. strigosus Muhl	...	a.c
Eriogonum longifolium Nutt	abc	abc
Euphorbia (*Chamaesyce*) sp	...	..c
Festuca octoflora Walt	...	a..
Fimbristylis caroliniana (Lam.) Fern	...	abc
Geranium carolinianum L	...	a.c
Gutierrezia dracunculoides (DC.) Blake	...	abc
Hedeoma hispida Pursh	...	a..
Hordeum pusillum Nutt	...	a..
Juncus interior Wieg	...	.b.
Leptoloma cognatum (Schultes) Chase	aBC	aBC
Lespedeza stuevei Nutt	aBc	abc
Linum rigidum Pursh	...	.b
Lithospermum angustifolium Michx	...	abc
Manisuris cylindrica (Michx.) Ktze	..c	ab.
Nothoscordum bivalve (L.) Britt	...	a..
Oenothera serrulata Nutt	abc	abc
Ophioglossum engelmannii Prantl	ab.	...
Oxalis stricta L	abc	abc
O. violacea L	a..	a
Panicum scribnerianum Nash	aBC	ABC
P. virgatum L	ABC	ABc
Paspalum pubescens Muhl	abc	aBc
Petalostemum purpureum (Vent.) Rydb	...	.bc
Plantago purshii R. & S	...	a..
P. virginica L	..	a..
Polygala incarnata L	...	.b.
Psoralea floribunda Nutt	ab.	ab.
Pyrrhopappus grandiflorus Nutt	...	a.c
Quercus prinoides Willd	abc	...
Rudbeckia hirta L	..	ab.
Ruellia humilis Nutt	abc	ab.
Solidago rigida L	abc	...
Sonchus asper (L.) Hill	...	..c
Sorghastrum nutans (L.) Nash	ABC	ABC
Specularia perfoliata (L.) A. DC	...	a..
Sporobolus asper (Michx.) Kunth	aBc	aBc
S. cryptandrus (Torr.) Gray	...	abc
Stellaria media (L.) Cyr	...	a..
Stylosanthes biflora (L.) BSP	...	.b.
Tephrosia virginiana (L.) Pers	a..	...
Tragia nepetaefolia Cav	ab.	...
Tridens flavus (L.) Hitchc	...	.bc
Vernonia baldwini Torr	...	abc
Viola rafinesquii Greene	...	a..
Total species	36	64
Exclusive species	11	37

Andropogon saccharoides, Aristida oligantha, Bromus catharticus, Buchloë dactyloides, Chloris verticillata, Festuca octoflora, Gutierrezia dracunculoides, Hordeum pusillum, Plantago virginica, and *Sonchus asper.*

The soil moisture in the first six inches of soil in the grazed pasture was slightly lower than that of the virgin prairie through the major portion of the growing season, while that of the third six inches was slightly higher (Table III). In all probability, most of these differences in the two levels were not significantly different on a statistical basis. The pH values for the soil in the grazed pasture were lower than those of the prairie in the spring but were essentially the same in the fall (Table IV). Organic carbon values for the grazed pasture were higher than in the virgin prairie (Table V). The volume-weight measurements were significantly higher in all cases in the grazed pasture than in the virgin prairie.

SEASONAL CHANGES

The greatest number of species per 25 quadrats was found in the spring in both plots (Table VII). Many of these are annuals which complete their life cycles and die early in the growing season although some are early flowering perennials.

The average per cent living cover was relatively low in the spring, reached its highest point in the summer, and was comparatively low in the fall (Fig. 1). The decreased living cover in the autumn, as compared with that in the summer, was due to the completion of life cycles of some species and the drying up of lower leaves of many of the remaining species.

In general, the oven-dry weight of the living material followed the same trends as the per cent of living cover for the individual plots (Fig. 2). However, no consistent correlations between living cover and oven-dry weight were evident. A comparison of Figures 1 and 2 shows that the virgin prairie exhibited not only lower living cover percentages but also lower oven-dry weights of living material than the grazed pasture during the spring and summer.

DISCUSSION

A total of 75 species was encountered in the in-

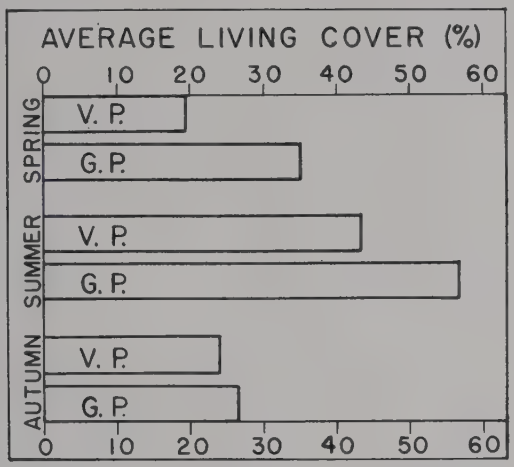

FIG. 1. Average per cent living cover in virgin prairie (V.P.) and grazed pasture (G.P.) for the 1950 growing season.

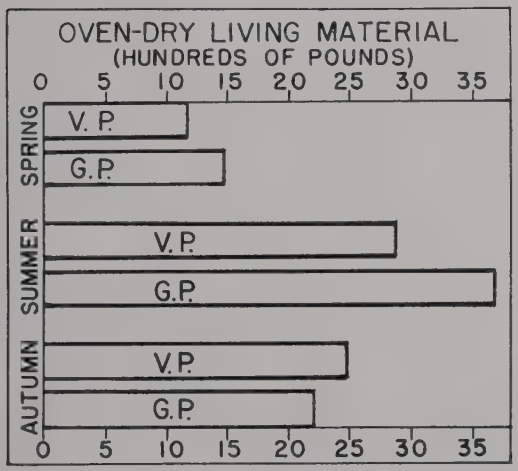

FIG. 2. Oven-dry weights of living material in virgin prairie (V.P.) and grazed pasture (G.P.) expressed in pounds per acre.

vestigation (Table VII). Although the species with a cover of 1.0 per cent or more were similar in the two communities (Table I), the composition of the grazed pasture was quite different from that of the virgin prairie. Of the total species found in the virgin prairie, only 39 per cent were encountered in the grazed pasture (Table VII). The numbers of exclusive species also indicate that the two communities were of different composition. The grazed pasture possessed many weedy species which are characteristic of disturbed areas.

The large amount of dead plant material found in the virgin prairie may be partially responsible for the low living cover percentages reported for this plot. According to Weaver and Fitzpatrick (1934), "Experiments over a period of only 3 to 5 years have shown that the accumulation of debris greatly retards growth in the spring. . . . Not only is there an actual diminution of the basal cover, but also certain of the smaller and earlier species are greatly handicapped and tend to disappear." The actual amount of dead material disposed horizontally over the soil appears to be the controlling factor. Seventy-five per cent of the superficial material in the virgin prairie is located in the first six inches above the ground. Much of this material lies flat on the ground, thereby providing an effective cover that would perhaps eliminate many seedlings.

When the cover percentages and oven-dry weights of living material are compared in the two plots (Table I and II, Figs. 1 and 2), it is evident that grazing has increased the total plant production. The most striking example is the tremendous increase in *Andropogon scoparius* with only slight decreases in most of the other important grasses. This suggests that moderate grazing increases the amount of forage in grasslands in central Oklahoma. This is further borne out by data obtained during the same growing season from a moderately grazed pasture (located across the road from the virgin prairie) that had been protected from grazing since the middle of the previous growing season. The oven-dry weights of living material (in pounds per acre) from the protected pasture were significantly higher than those of the virgin prairie at all three sampling periods (Spring, 1650; Summer, 4264; Autumn, 3987). Dyksterhuis and Schmutz (1947) have reported very low yields of green herbage in a relict area with considerably higher yields in a meadow and on range lands. It is of interest to note that they also found the greatest amount of natural mulch (dead material) in the climax area.

The effects of grazing on grasslands in central Oklahoma fall into two categories: (1) the effects on the vegetation, and (2) the effects on the soil. Obviously, the effects are closely related and one would not expect a change in the soil to occur without some change in the vegetation. Several edaphic factors—soil moisture, pH, organic carbon, and volume-weight—were measured in the two plots. Although some interesting data were obtained on the above factors, no significant correlations could be found between the changes in vegetation and the soil factors in question.

Few large differences in soil moisture were encountered in the two plots (Table II). This was undoubtedly due to the abundance of rainfall during the summer. Certain trends of decreased soil

moisture in the pasture could be detected during various periods of the growing season in the first six inches of the soil. It is entirely likely that moisture would become a limiting factor in this plot during unusually dry years.

The reasons for the lower pH values obtained in the spring for the grazed pasture soil was not evident (Table IV). The leaching of basic ions by excessive precipitation could not be used as an explanation since the lowered pH did not occur in both plots and since the precipitation was below normal for the few months preceding the sampling. A contributing factor could have been the action of microorganisms on the organic matter in the soil but it seems improbable that this action would be solely responsible for the lower pH values.

The pH values obtained in this investigation are in fair agreement with those obtained by other investigators in Oklahoma. Daniel *et al.* (1943) reported values for virgin soil in north central Oklahoma of pH 5.8 to 6.4 for the surface layers and of 7.8 to 8.1 for subsurface layers. Gernert (1936) in north central Oklahoma, reported values for 6.28 for the first three inches of soil in roadside (relict) grassland and pasture areas. Slightly lower values were reported in experimental plots subjected to various degrees of clipping.

In spite of the fact that there was more dead material found on the ground in the virgin prairie than in the grazed pasture, the organic carbon content of the soil itself was much higher in the grazed pasture (Table V). There may be, therefore, little relationship between the amount of superficial organic matter and the content of organic carbon in the soil. Cover percentage of living plant material was much higher in the grazed pasture than in the virgin prairie. In most cases, with more living material above the ground, one would find more roots and hence more organic carbon in the soil. Aldous (1934) suggested that increases in organic matter in pasture areas that he studied were due to the increased root systems instead of the increase of organic matter on top of the soil. Gernert (1936) reported higher organic matter values in pastures subjected to frequent clipping (and the clippings removed) than in grasslands along the roadside (relict areas) in north central Oklahoma. However, he found the greatest root weight in the unmolested roadside grassland and concluded that organic matter is apparently not associated with the amount of live roots and suggested that "if soil organic matter is quite permanently residual, it must be the result of previous vegetative growth."

Values obtained for organic carbon in this investigation agree, in general, with those obtained by other workers. However, no strictly comparable data were found. Nease (1948) reported an average value of 1.05 per cent (Walkley and Black) for the organic carbon content of the surface layers of soil in an overgrazed pasture in south central Oklahoma. Aldous (1934) found organic carbon values for the first six inches of the soil of 2.44 to 2.47 per cent in ungrazed pasture areas and 2.21 to 2.49 per cent in slightly grazed areas in western Kansas. No mention was made of the method used in these determinations. Weaver and Bruner (1948) reported organic matter values (Walkley and Black) that ranged from 4.38 to 5.17 per cent (equivalent to 2.04 to 2.40 per cent organic carbon) in the first four inches of the soil in pastures in Nebraska.

Volume-weight measurements indicate that the soil in the virgin prairie has a more desirable structure in that it is not as compact as the soil in the other plot. These data indicate that grazing increases the volume-weight or compaction of the soil.

Several workers have used volume-weight measurements to compare various soils. Nease (1948) compared relict prairie areas which had not been subjected to grazing, with a secondary tall-grass prairie and found that the soil was 31 per cent more compact in the secondary tall-grass prairie than in the relict prairie. Alderfer and Merkle (1941) compared soils in Pennsylvania and found that the volume-weight of blue-grass sod was lower than that of cultivated plots. Auten (1933) compared volume-weights with real specific gravity and concluded that porosity differences in forest and field soils are caused more by soil structure than by organic matter content. He found that grazing and fire reduced porosity (increased volume-weight).

It is evident from the above data that more work must be done before any conclusions can be drawn on the relationships of soil factors to vegetation in grasslands in central Oklahoma.

Summary

This investigation deals with an analysis of the vegetation of two grassland plots: a small virgin prairie and a grazed pasture, in McClain County in central Oklahoma.

The dominant grasses in the virgin prairie were *Andropogon scoparius, Panicum virgatum,* and *Sorghastrum nutans. Andropogon gerardi* probably should be included in the dominants of this plot. *Andropogon scoparius* and *Sorghastrum nutans* were the dominants in grazed pasture. The data indicate that *A. scoparius* appears to be favored by moderate grazing of the pasture.

A smaller number of species and a lower aver-

age living areal cover was found in the virgin prairie than in the grazed pasture. Total weight of living plant material was higher in the grazed pasture than in the virgin prairie. However, total weight of dead plant material was lower in the grazed pasture than in the virgin prairie. No consistent correlations were found between the total living cover and the weight of the living material in either of the plots.

Soil moisture did not become a limiting factor during the 1950 growing season. Certain trends suggest that the soil in the grazed pasture dries out much more readily than in the virgin prairie.

Minor fluctuations were found in the pH determinations in the two plots. No correlation could be found between pH and any other soil factor studied.

The percentage of organic carbon in the soil was lower in the virgin prairie than in the grazed pasture. The amount of organic carbon seems to be related to the quantity of living plants, and not to the mass of dead plant material.

Volume-weight values were markedly lower in the virgin prairie than in the grazed pasture.

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FURTHER STUDY OF THE TREE-HOLE COMPLEX WITH EMPHASIS ON QUANTITATIVE ASPECTS OF THE FAUNA

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INTRODUCTION

A tree hole is any tree cavity, produced through the action of extrinsic factors, that is in direct contact with the external environment at some point in its development. Tree holes have received relatively little attention from ecologists. Recently (Park, Auerbach, and Corley 1950) tree holes were classified; physical and biotic factors important in the origin and development of such habitat niches discussed; the tree-hole microsere concept developed; and a start made in a study of the tree-hole food web and pyramid of numbers. In this initial paper the research emphasis was on the populations of beetles of the family Pselaphidae that inhabit tree holes.

The present report is another small step in the accumulation of data and ideas concerning this relatively small, delimited habitat niche. Such biotopes are more easily studied than, say, the floor stratum of a forest, although the tree hole may be thought of as a discontinuous extension of the forest floor (Allee, Emerson, Park, Park, and Schmidt 1949, p. 486). It has a population of log mold animals if it be in the terrestrial phase of the microsere, and this population tends to increase in size and taxonomic diversity as its walls soften, and the cavity begins to fill with litter. This makes for increase in ecological complexity as well. The tree hole also has its particular type of microclimate, yet one that is correlated with the more fluctuating microclimate of the whole forest community. In such tree-hole populations the oribatid mites and the collembolans usually are the most numerous arthropods, again, in parallel with the abundance of these two groups in forest floor leaf mold and log mold. All of these organisms are inextricably involved in the Darwinian web-of-life of the major community.

ACKNOWLEDGMENTS

Even within the confines of such a small habitat as the tree hole, the taxonomic aspects present a great problem. Any sound community analysis is eventually based upon an impeccable taxonomy since physiological demands and ecological requirements must be related to kinds of organisms. Since species are the community building blocks, their populations must be named. Whereas the senior author is familiar with pselaphid beetles and the junior author with centipedes, the other groups had to be sent off to specialists for determination. Consequently, the authors are greatly in the debt of many people and these latter are as follows:

Dr. Earl Auerbach, American Meat Institute, Chicago, Illinois (Protozoa); Dr. William Balamuth, University of California (Protozoa); Dr. R. V. Chamberlin, University of Utah (Chilopoda, in part); Dr. Tom Daggy, Davidson College, North Carolina (Coleoptera larvae); Mr. Henry Dybas, Chicago Natural History Museum (Ptiliidae, Murmidiidae, Euglenidae, Lathridiidae); Dr. Robert Gregg, University of Colorado (Formicidae, in part); Dr. C. C. Hoff, University of New Mexico (Pseudoscorpionida); Dr. Harlow Mills, Illinois Natural History Survey (Collembola, Protura); Dr. G. H. Mickey, Northwestern University (Drosophilidae); Dr. Charles Seevers, Roosevelt College, Chicago (Staphylinidae); Dr. M. R. Smith, U. S. Bureau of Entomology (Formicidae, in part); Dr. Luella M. Walkley, U. S. Bureau of Entomology (Ichneumonidae); Mr. Rupert Wenzel, Chicago Natural History Museum (Histeridae, Corylophidae); Dr. Paul Winston, University of Colorado (Carabidae, in part).

We are also indebted to Dr. Gwendolyn Jones, of our Department, for weighing out special mold samples for the rhizopod survey, and the authors are particularly grateful to Professor Thomas Park, of the University of Chicago, for a critical reading of the manuscript and numerous helpful suggestions.

MATERIALS AND METHODS

Between March 18, 1950, and April 19, 1952, eighteen tree holes were studied quantitatively. The field data usually included the following: (1) species of tree, except in the case of hybrid oaks where identification was not feasible; (2) whether the tree was alive or dead; (3) height of tree-hole orifice above ground, and shape, size and direction in which the orifice faced; (4) size, shape and condition of tree-hole; (5) overt evidence that the hole was occupied, or had been occupied by mammals; (6) photographs of the tree-hole orifice.

Such mold samples were first weighed wet to within twenty-five grams, and then placed in

modified Berlese equipment. This consisted of a series of large funnels of heavy gauge galvanized iron. Each funnel was eighteen inches deep, including a three and a half inch spout, and measured twelve inches in diameter across the top, and the orifice with a one inch diameter. Circular screens of heavy hardware cloth were used to retain the mold. These screens had interstices of one-fourth inch square. Where the mold was exceptionally fine-grained two screens were used or a thin layer of excelsior or more or less intact leaves and debris were first placed on the screening. The heat source was an electric light bulb. The bulb was in a heavy enameled shade that measured twelve inches in diameter, so that a good fit between shade and funnel lip was secured. The power of the bulb varied between a low of sixty to a high of one hundred and fifty watts.

From previous experience, it was found that no set time for berlesing a sample could be relied upon within reasonable limits. Instead, each sample was berlesed until no more arthropods could be expelled. This necessitated frequent changes in the berlesate.[1] The berlesate consisted of those organisms that dropped from the spout orifice of the funnel into a beaker of 95% ethyl alcohol. The number of berlesates required for a given mold sample varied from one to fifteen. The time for this extinction point to be reached varied as a consequence of size of sample, water content and condition up to a maximum of 1071 hours of berlesing time. In general, the size of the bulb used was a factor, but bulbs of lower wattage were found to be more desirable as they did not dry out the mold as rapidly and a more accurate yield could be anticipated. In fact, the general Berlese method is desirable in such quantitative work but has its drawbacks. For example, although it is satisfactory for extraction of arthropods from tree-hole mold, it is not a satisfactory method for estimating populations of gastropods, oligochaete worms, nematodes and other taxonomic groups. Care must be taken, in the case of arthropods, that the sample is warmed slowly and over a sufficient time interval. A partial check on the efficiency of the method was the examination of small bits of mold under a dissecting binocular at 70 diameters, near the extinction point of the berlesate, to determine whether living or dead arthropods could be found in the mold. This was done on three occasions with negative results so that it was felt that a great majority of the arthropods had been expelled. The general aspects of the use and misuse of the Berlese-Silvestri-Tullgren automatic method of extracting organisms has been discussed by Strickland (1947), Fenton (1947) and Macfadyen (1953), among others, and needs no elaboration in a paper of this sort.

When the probable extinction point had been reached or approximated, the mold sample was reweighed. The weight loss represented primarily evaporation of free water. This weight loss was always expressed in per cent of the initial wet weight since the wet sample weights varied widely.

Excess alcohol was decanted from the berlesate, and the remainder examined. A portion of the latter was poured into a counting frame. This frame was made by drawing a series of parallel horizontal and vertical lines across the bottom of a petri dish with a seven-centimeter diameter. The resulting dishes had about eighty-six small squares.

The small amount of berlesate examined at a given time allowed the contained arthropods to be sorted and counted with reasonable accuracy. This process was laborious. Too much debris, *e.g.*, mold grains, rendered the examination more difficult and more subject to error. If so much mold had fallen from the funnel that the organisms were obscured, the mold was either picked out, smaller samples examined, or flotation was employed. This latter consisted in decanting almost all of the alcohol from the berlesate, then pouring in water. This caused the dehydrated organisms to float to the surface. The latter was decanted into enough alcohol to cause them to sink to the bottom, and then the process could be begun with less debris.

This general process was followed for the arthropod census. In one sample a quantitative census was made of tests of dead rhizopod protozoans. In this case the minute mold samples were weighed out on a chemical balance.

Faunal Tree-hole Checklist

The following list includes rhizopods and arthropods only. Where identification could not be secured with accuracy the next highest taxonomic category was employed. In the case of insects, adults are not so indicated but larvae are always noted as such.

Protozoa
- Rhizopoda
  - **Testacea**
    - Difflugiidae
      - *Difflugia arcula* Leidy
    - Euglyphidae

Arthropoda
- Crustacea
  - **Isopoda**
    - Porcellionidae
      - *Trachelipus rathkei* (Brandt)

[1] The term berlesate ("ber-*laze*-ate") as used here is intended to save words. Others may have so employed it, and to our knowledge it has been used once previously (Park 1953, p. 1).

Oniscidae
Oniscus asellus Linnaeus
Arachnida
Phalangida (immature)
Pseudoscorpionida (Chelonethida)
Chernetidae
Microchernes dentatus (Banks)
Acuminochernes crassopalpus (Hoff)
Chthoniidae
Chthonius tetrachelatus (Preyssler)
Cheiridiidae
Cheiridium firmum Hoff
Arachnida (immature spiderlings)
Acarina
Mesostigmata
Parasitidae (and allies)
Uropodina
Trombidiformes
Bdellidae
Myobiidae
Trombidiidae
Trombidium
Trombiculidae
Oribatei
Chilopoda
Lithobiomorpha
Lithobiidae
Lithobius forficatus Linnaeus
Garibius
Simobius gardneri Auerbach
Tidabius
Scolopendromorpha
Cryptopidae
Cryptops
Geophilomorpha
Schendylidae
Schendyla nemorensis (C. Koch)
Soniphilidae
Poaphilus
Linotaeniidae
Linotaenia
Diplopoda
Julidae
Insecta
Protura
Acerentomidae
Acerentulus
Acerentomon
Eosentomidae
Eosentomon
Thysanura (Suborder Entotrophi)
Campodeidae
Collembola
Poduridae
Entomobryidae
Sminthuridae
Orthoptera
Blattidae
Corrodentia
Atropidae
Psocidae
Thysanoptera
Heteroptera
Tingidae
Homoptera
Cicadellidae
Erythroneura comes Say
Neuroptera
Ascalaphidae

Coleoptera
Carabidae
Agonoderus pallipes (Fabricius)
Bembidion
Calosoma scrutator (Fabricius)
Clivinia
Dicaelus (larvae)
Platynus
Tachymenis flavicauda (Say)
Catopidae
Catops terminans (LeConte)
Scydmaenidae
Acholerops
Connophron debilitans Casey
larvae
Corylophidae
Orthoperus
Staphylinidae
Aleocharinae (larvae)
Atheta
Omaliinae (larvae)
Omalium
Piestinae
Thoracophorus costalis Er.
Staphylininae (larvae)
Philonthus
Quedius
Xantholinus gularis LeConte
Xantholinus (near *sanguinipennis* LeConte)
Tachyporinae
Bryoporus
Conosoma
Tachinus
Pselaphidae
Batrisodes globosus (LeConte)
Euplectus confluens confluens LeConte
(adults and ?larvae)
Euplectus confluens iowensis Casey
Euplectus interruptus LeConte
Melba
Thesium cavifrons (LeConte)
Ptiliidae
Acratrichis
Micridium
Ptenidium
Pteryx
Ptiliolum
Histeridae
Aeletes
Bacanius misellus LeConte
Bacanius
Carcinops 14-striata Steph.
Dendrophilus opacus Ross
Dendrophilus punctatus Hbst.
Dendrophilus xavierae Lewis
Epirus pulicarius Erichson
Hololepta (larvae)
Isolomalus seeversi Wenzel
Xestipyge conjunctum (Say)
Anthicidae
Notoxus
Euglenidae
Elateridae
Cardiophorinae (larvae)
Elaterinae
Agriotini
Agriotes (larvae)
Elaterini
Elater (larvae)

Elater obliquus Say
Melanotini
Melanotus (larvae)
Steatoderini (larvae)
Pyrophorinae
Lepturoidini (larvae)
Pyrophorini
Aeolus dorsalis (Say)
Dermestidae
Anthrenus museorum (Linnaeus) (larvae)
Cucujidae
Laemophloeus biguttatus Say
Rhipiceridae
Zenoa picea (Beauv.) (larvae)
Alleculidae
Capnochroa fuliginosa (Melsh.) (larvae)
Hymenorus (larvae)
Cryptophagidae
Loberus impressus LeConte
Cryptophilus integer (Heer)
Anchicera
Colydiidae
Cerylon castaneus Say
Silphidae
Ptomaphagus pusio LeConte
Mycetophagidae
Mycetophagus flexuosus Say
Murmidiidae
Lathridiidae
Cartodere
Melanophthalmus
Metophthalmus parviceps LeConte
Tenebrionidae
Platydema ruficorne Sturm
Tenebrio picipes Hbst. (adults and all larval instars)
Cisidae
Cis
Ceracis sallei Mell.?
Xestocis
Trogidae
Trox
Chrysomelidae
Glyptina
case-bearing larvae
Cantharidae
Cantharinae (larvae)
Curculionidae

Lepidoptera (larvae)

Hymenoptera
Belytidae
Tenthredinidae
Ichneumonidae
Ceraphronidae
Ceraphron
Formicidae
Aphaenogaster tennesseensis Mayr
Lasius
Lasius umbratus aphidicola (Walsh)
Leptothorax curvispinosum ambiguus Emery
Monomorium floricola (Jerdon)
Ponera coarctata pennsylvanica Buckley
Strumigenys pulchella Emery

Diptera
Cecidomyidae
Drosophilidae
Drosophila
Mycetophilidae
Sciarinae
Stratiomyidae
Syrphidae

Siphonaptera
Hystrichopsyllidae
Epitedia wenmanni (Rothschild)?

This taxonomic census has required the considerable time of many people and yet is very far from complete. In such groups as Acarina and Collembola it is unlikely that determinations will ever approach completion. Consequently in quantitative comparisons made later the lowest category will be used, even if it be a large group of species.

In this census the arthropods are represented by 5 classes, 23 orders, 67 families, 93 genera, and 51 identified species. Four species are new to science and are being described by the appropriate specialists, or descriptions have appeared (Auerbach 1950; Hoff 1952).

As noted later, these animals include a large majority of herbivores, numerous predators, and quite a few ectoparasites. Appearance of the latter in berlesates often throws light on the kind of vertebrate that was occupying the tree hole. For example, the flea, *Epitedia wenmanni,* was in the berlesate of a tulip tree in southern Illinois. Earlier in the year, flea larvae were in the berlesate of the same tree hole. Ewing and Fox (1953) give the common deer mouse, *Peromyscus leucopus,* as the host mammal.

The same kind of suggestion is given by the appearance of large numbers of the parasitic mites, Myobiidae, in the berlesate of a beech tree hole in southwestern Michigan. Baker and Wharton (1952, p. 230) list Rodentia, Insectivora, and Chiroptera as the hosts of these mites.

In this same beech tree-hole berlesate appeared larvae of the dermestid *Anthrenus museorum* (Linnaeus), common beneath spider webs, and in bird and mammal nests, as well as in museum collections.

These few instances are cited here since they serve to show how taxonomy and ecology are mutually helpful. This relationship is less obvious in the condensation of details in a table.

Similarly in the course of study, preparation of material for exact identification may lead indirectly to valuable data on ecological matters. For example, in the study of ptiliid beetles cleared microscope slides are essential; such slides showed spores of fungi in the digestive tracts of these beetles.[2] The feeding habits of Ptiliidae are not known with certainty. It has been thought that they were herbivorous in general; these slides suggest that the beetles, of several genera, had been feeding on fungi, or at least had been feeding on the fungus-infested tree-hole mold.

[2] Personal communication from Henry Dybas.

Interesting information on zoögeography is also brought out. Thus the pseudoscorpion family Cheiridiidae has never been reported from the region of investigation before (Hoff 1949). The family was represented abundantly in the berlesate of the tulip tree hole noted earlier. This tree was in Lawrence County, in southern Illinois, and Dr. Hoff[3] informs us that this is the first report of the family in the central United States, and that these arachnids appear to be closely allied to a genus reported from South Africa and Formosa.

Of local interest is the small pselaphid beetle, *Euplectus interruptus*. This species appeared in fair numbers in the berlesate of an oak tree hole in Carlé Woods, Cook County, Illinois. Although the species is known from forest floors in neighboring areas, it is the first record for the Chicago Region, an area in which the pselaphids have been sought for with vigor for some twenty years.

The general conclusion would seem to be that if one wishes to make a contribution to science and at the same time have a stimulating series of experiences, he could do little better than study tree holes.

The Rhizopod Population

The original plan of this study was the quantitative comparison of the arthropods of a series of tree holes. In the course of checking both mold samples and berlesates, both for efficiency of the method and for determination of the extinction point, it came as a surprise to the authors to find the tests of rhizopod protozoans.

Although the protozoan fauna of the soil is large and varied, and although tree-hole mold is a discontinuous extension of the forest floor log mold, protozoans in tree holes are not expected as consequence of their minute dimensions and the realization that the method used to extract arthropods is not suitable to the protozoölogist.

Nevertheless, one should be prepared to anticipate such an event when it is realized that under proper conditions a tree hole may be filled seasonally or permanently with water, and consequently its ecological history parallels that of a temporary or a permanent pond (Park, Auerbach, and Corley 1950).

Their presence in the berlesate is considered a matter of chance, *e.g.*, they were dead when the sample was collected, or they were killed by the method used, and the tests adhered to a mold grain and eventually fell into the berlesate. Once their presence was noticed, it was possible to estimate their abundance by direct examination of the mold sample.

Of interest is the method of rhizopod colonization of tree holes. The explanation that most readily comes to mind is that encysted testaceans are wind-dispersed, and under favorable conditions such encysted individuals may be blown through the tree-hole orifice. Once in the mold, moisture conditions being suitable, there would appear to be no obstacle to their feeding and building up the rhizopod population.

This would explain the presence of such organisms in tree holes well above ground. In the case of basal tree holes, or tree holes above ground but with cavities that extended into the floor or subterranean strata, such wind-driven encysted forms would not be needed, rather the soil testaceans might emigrate into the mold and thrive.

One mold sample contained such large numbers of a testacean that the tests began appearing in every portion of the berlesate examined. The tests were those of *Difflugia arcula* Leidy (Fig. 1), and were in the mold from tree hole No. 9, near Ramsey, Bergen County, New Jersey. The tests were firmly embedded in the dried mold in the berlesed sample and consequently those few that fell into the berlesate could not be relied upon to obtain a quantitative estimate of the population.

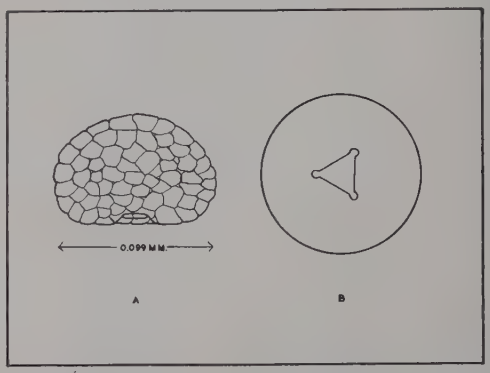

Fig. 1. An unreported tree-hole resident, the rhizopod, *Difflugia arcula* Leidy. A. Test in lateral view. B. Outline view of ventral surface of test.

Four small pieces of dry mold, from different parts of the sample, were collected and weighed out to 33.4 milligrams. These mold bits were then transferred to the counting frame and soaked until they could be torn apart. In this way the mold was separated into a powdery, evenly distributed mass. The tests were very obvious against this background and were counted in high illumination at 70 diameters. Assuming that the rhizopods were randomly distributed, there were 174 tests in the 33.4 milligrams of tree-hole mold. This gave an estimate of 1.91 tests per milligram; 1,910 tests per gram; 1,910,000 tests per kilogram.

[3] Personal communication from C. Clayton Hoff.

TABLE I. *Tree Holes Studied.*

Tree hole	Location	Species of tree	Free water content of mold (%)	Population density of		
				Anthropods per kilogram of mold	Acarina %	Collembola %
1	Geneseo Henry Co., Illinois	?	54	2,700	90.4	4.9
2	Pinkstaff, Lawrence Co., Illinois	Tulip (*Liriodendron*)	50	4,700 (2,400)	79.3 (60.0)	11.0 (20.0)
3	Lake Wales, Polk Co., Florida	Grapefruit	5.2	5,400	3.4	16.0
4	Mayo, Lafayette Co., Florida	Live Oak	20	7,600	24.4	72.4
5	Milwaukee, Milwaukee Co., Wisconsin	American Elm	52.3	3,700	95.2	4.0
6	Milwaukee, Milwaukee Co., Wisconsin	White Oak	46	1,600	50.8	23.9
7	Naylor, Prince Georges Co., Maryland	Red Oak Group	59	1,300	55.7	27.4
8	Highland Park, Lake County, Illinois	Apple	85	1,700	80.4	13.2
9	Ramsey, Bergen Co., New Jersey	Oak	57	260	84.8	2.4
10	Geneseo, Henry Co., Illinois	American Elm	75	850	66.8	2.4
11	Greenwich, Fairfield Co., Connecticut	Crabapple	53	1,800	85.5	4.9
12	Monon Springs, Putnam Co., Indiana	American Elm	85	2,200	94.5	0.8
13	Evanston, Cook Co., Illinois	Catalpa	47	100	84.1	0.4
14	Mill Creek, Tehama Co., California	Sugar Pine	38	2,100	55.8	34.9
15	Turkey Run, Parke Co., Indiana	Wild Black Cherry	57	2,000	76.6	13.1
16	Lakeside, Berrien Co., Michigan	Beech	67	15,800 (8,500)	85.5 (73.0)	9.0 (18.0)
17	Skokie, Cook Co., Illinois	Silver Maple	42	480	96.0	2.4
18	Des Plaines, Cook Co., Illinois	Oak	60	1,400	89.0	6.0

Considering the known tendencies of animal numbers to fluctuate, this datum gives some idea of the potential organismal population density in a well-stocked tree hole. If there can be nearly two million individuals of such a large rhizopod as *Difflugia arcula* per kilogram, the numbers of smaller protozoans, nematode worms, fungi and bacteria are probably prodigious.

The tree-hole habitat may represent an unreported niche for *Difflugia arcula*. If so, it is not a surprising one since this species is reported from sphagnum swamp, moss and soil by Kudo (1931, p. 237), and Calkins (1926, p. 339) observes that many of the Testacea lead a semiterrestrial life and "abound in moss and similar damp places." In his classic treatise on soil protozoans, Sandon (1927) finds many species have an almost cosmopolitan distribution in soils over the world, that the testaceans thrive in moist soil, and that there are few that live in deep soil or subsoil, the majority being found within the top twelve centimeters.

THE ARTHROPOD POPULATION

Only a partial analysis can be given for the large and diversified arthropod population of tree-hole mold. Incomplete taxonomy is a major difficulty. Lack of precise information on the ecological requirements of the several species is another major drawback.

The eighteen tree holes studied can be summarized (Table I) to bring together certain general aspects.

Factors that affect population density in tree holes

1. *New generations.* Useful as were the methods used in this study, certain factors must be evaluated with care. The berlesing of tree-hole mold should be continued to the extinction point to arrive at an accurate concept of the population present when the sample was placed in the apparatus. Often this means an extended berlesing period. If the collected sample contained the adults, as well as eggs or larvae/nymphs of the next generation when the latter immature stages were about to hatch, then in the course of berlesing, the adults of the first generation would be counted early in the berlesate, and subsequently the new generation would appear in the berlesate. This would give an exceptionally high population density. In nature the adults would probably be on the wane when the new generation appeared, or at least this would be the situation when the new generation reached maturity. It should be remembered that this may not be necessarily true,

viz., in nature the parent population might normally overlap one or more generations of offspring.

This is on the assumption that it is the standing crop of adults that is desired. If the potential crop is desired, then these later additions are not out of place. It must also be remembered that the heat of the sample under treatment may act as an accelerative influence speeding up the date of development from egg to adult. Similarly, the season collecting date is a factor.

In the present study one of the objects was to arrive at population estimates of equal weights of tree-hole molds in a variety of trees and tree holes. What was wanted were the number of adults of a species, and if feasible, the number of immature individuals of the same species present at a given time in the mold.

The Berlese method is not at fault here. The obvious remedy is to count the organisms in the berlesate by fractions over the period of berlesing to extinction point. This course was followed.

In two tree-hole samples (Nos. 2 and 16) a new generation of mites appeared during the berlesing period. A glance at Table I will show that these samples have high population densities per kilogram of mold.

Sample 2 had successive berlesate counts of Oribatei as follows: 1162 (41 hours), 172 (90 hours), 159 (111 hours), 140 (137 hours), 193 (159 hours), 651 (184 hours), 1430 (212 hours), 1473 (236 hours), 339 (257 hours), 314 (280 hours), 211 (303 hours), 116 (326 hours), 48 (350 hours) and 12 (374 hours). In other words, in 374 berlesing hours a total of 6420 oribatid mites fell into the alcohol from an initial sample weighing wet 1980 grams. Of this total, there were 1,826 mites at 159 hours and with abrupt onset a new generation began appearing in the berlesate, *e.g.,* 4594 mites between 159 and 374 hours.

With such information the berlesate population density can be graphed against berlesing hours and the population peaks can be easily seen, or the tabular data can be corrected.

Such data have another use. The adults resident in the mold when the sample was collected numbered about 2000. The new mite generation (of many families, genera and species) numbered some 4,500. Perhaps this second, larger figure is that of the new generation before natural death, predation and parasitism had reduced the standing crop, *e.g.,* the figure represents the initial potential.

Finally, it must be emphasized that too much care cannot be used in collecting the data and in its interpretation. It is difficult for non-acarologists such as the authors to determine what is a sexually mature adult and what is one of the several nymphal stages in oribatid mites. It is impossible for the authors to identify these mites even to family, especially since the "Oribatidae" of, say Banks (1915) is now an assemblage of some thirty-five families (Baker and Wharton 1952).

True population studies on these and other arthropod groups, then, must be done by specialists who can separate the life history stages with accuracy, and can identify to species the several mite populations involved. This was not attempted in the present report. Instead, the appearance of a new generation was noted and the organisms counted as "oribatoid mites," whether immature or mature. This allowed correction factors to be made.

Sample 16 involved the appearance of a new generation of mites, but the situation was different. The mites were not oribatids but ectoparasitic trombidiforms of the family Myobiidae, and very large numbers of parasitid and uropodid mites.

In Table I, sample 2 has a standing crop population density per kilogram of 2,400; Acarina 60 per cent; Collembolans 20 per cent. Similarly, sample 16 has a standing crop density of 8,500 per kilogram; Acarina 73 per cent; Collembola 18 per cent. These corrected values appear in Table I in parentheses.

2. *Ants.* The presence of formicids in tree holes may have a positive or negative effect upon the total population density per weight or volume of mold.

If the sample is collected, usually unwittingly, in a tree hole that houses a large ant nest, the total population density may be high but the worker ants will form the majority of the arthropods in the berlesate. This is obviously the case in tree hole sample No. 3 (Table I). In this sample, out of a total of 3,082 arthropods in the berlesate, there were 2,386 worker ants of *Monomorium floricola,* or 77.4 per cent of the total census.

On the other hand, as ants increase in tree holes, there is a tendency for other tree-hole occupants to decline in numbers as pointed out earlier (Park, Auerbach and Corley 1950). Sample No. 3 is a case in point, with the mites reduced to 177 per kilogram, *i.e.* far below the average participation by this group (Table II).

3. *Nesting Mammals.* Although nesting deer mice or squirrels may increase substantially the number of arthropods in a tree hole as a consequence of their ectoparasites (mites, lice, fleas), much use of the hole tends to reduce the normal numbers of tree-hole arthropods. Tree-hole sample No. 13 illustrates this effect. Gray squirrels were seen frequently running into and out of this

TABLE II. *Comparison of Arthropod Orders.*

Arthropod Order	Percentage frequency in 18 tree holes	Average population density per kilogram of wet mold	Average percentage of total population of sample
Isopoda	16%	2.0	0.08
Lithobiomorpha	44%	3.0	0.12
Scolopendromorpha	11%	2.0	0.08
Geophilomorpha	11%	0.5	0.02
Juloidea	27%	20.0	0.80
Pseudoscorpionida	22%	18.0	0.72
Phalangida	5%	0.5	0.02
Acarina	100%	1515.0	61.20
Araneida	44%	3.0	0.12
Protura	16%	11.0	0.44
Collembola	100%	674.0	26.96
Thysanura	11%	1.0	0.04
Orthoptera	5%	14.0	0.56
Neuroptera	5%	0.5	0.02
Corrodentia	38%	16.0	0.64
Thysanoptera	27%	16.0	0.64
Heteroptera	27%	3.0	0.12
Homoptera	11%	1.5	0.06
Coleoptera	100%	80.0	3.20
Lepidoptera	11%	1.5	0.06
Diptera	88%	79.0	3.16
Siphonaptera	5%	0.5	0.02
Hymenoptera	83%	15.0[4]	0.60

[4]Adjusted as a consequence of the large ant nest in tree hole No. 3; with this nest included, the average would be 389 ants per average kilogram of tree hole mold, which is not in accord with reality.

tree hole, and although the acarinid percentage is high, this included parasitic mites that made up 65.3 per cent of the total berlesate. The population density as a whole is very low at 100 per kilogram of mold.

Three biotic influences that affect the arthropod population of tree holes have been mentioned briefly. Physical factors also play an important rôle, both in the initiation and development of the habitat niche (Park, Auerbach and Corley 1950), and in their effect upon the population density of tree-hole arthropods.

4. *Water content of the substrate.* The free water content of the mold is a very important physical factor in this biotope.

Dry mold and high ant density apparently are operating together to reduce the mite and collembolan populations in tree hole No. 3. This is an exceptional condition, in as much as the mold is usually moist.

Table I deals with 18 tree holes, the collected samples of which were taken at different times of the year and in different parts of the United States. In this table the average water content is 53 per cent.

Park, Auerbach, and Corley (1950) studied twenty-seven tree-hole samples, and the average water content was 59 per cent.

If the forty-five tree holes noted are examined for percentage distribution of free water content, then we find that there are 2 samples (0-10% water content), 2 (11-20%), 1 (21-30%), 2 (31-40%), 6 (41-50%), 11 (51-60%), 8 (61-70%), 8 (71-80%), 4 (81-90%), and 1 (91-100%). In these the lowest was 3 per cent, the highest was 90 per cent, and the average was 57 per cent.

This suggests, but does not prove, that samples with greater than 50% water are more frequent than those with less than 50% water. The tree holes were not selected for water content, and some samples were sent to the authors, well-packed to deter moisture loss, whereas others were collected locally and processed within a few hours after collection.

Quantitative Comparison of Arthropod Orders

In the next place it is of interest to contrast the densities of the several arthropod orders sorted from the berlesates. This is attempted in Table II.

Table II summarizes the analysis of eighteen tree-hole mold samples at the level of the order. Twenty-three orders are represented, of which one is crustacean, three chilopod, one diplopod, four arachnid, and fourteen hexapod. With respect to the frequency with which any given order occurred in the eighteen samples, it will be noted that three orders (Acarina, Collembola, Coleoptera) were found in every sample, and two additional orders (Diptera and Hymenoptera) occurred in the large majority of the samples.

The third column of the table lists the average number of individuals in each order for the eighteen samples. These data are rounded-off numbers, based on actual population counts that have been averaged for all of the samples. The authors are aware that eighteen samples are not as good as fifty, and that fifty would not be as good as one thousand. This statistical description of the average kilogram of wet tree-hole mold given here is believed to approximate the average conditions in nature.

The fourth column is concerned with the conversion of these population data into percentages of the whole. The average kilogram was found to contain 2,477 arthropods, including immature stages and adults, but not pupae. Of this total, two of the orders with the highest frequency of occurrence, the Acarina and Collembola, make up 88 per cent of the population.

Several interesting observations can be discussed. The Orthoptera occurred only once but in this instance they were sufficiently abundant to nearly equal the average number of Hymenoptera, although the latter were found in 15 of the 18 samples. This illustrates the aggregative tendencies of certain groups, *e.g.*, cockroaches, but also illustrates the point that with many more samples

available such local concentrations would not bulk so large in the percentage totals.

The Heteroptera occurred in five samples, and in four of these were represented by the family Tingidae, and in the fifth by an unidentified nymph. This suggests that the lace-bugs are adjusted to the tree-hole environment, and may pass inactive periods in the biotope. Since they suck the sap of leaves from the shrub and tree strata they are conveniently stationed.

Both records of Homoptera were of the common cicadellid genus, *Erythroneura,* another herbivore of the herbaceous, shrub and tree strata during the growing season, and quite common in early spring in the litter of protected forest floors.

The Phalangida were found in but one sample. This was a surprise, since phalangids are often found in tree holes, and often in numbers, clinging to the wooden walls or vibrating when disturbed. This may be another instance of insufficient data, or it may be that the Berlese method is not adapated to accurate estimation of these arachnids.

The Lepidoptera occurred only as larvae.

Diptera were represented also chiefly in the larval stage. Of 1,275 dipterans taken in the eighteen samples, only 34 were adults, usually adult mycetophilids, or fungus-gnats.

Hymenoptera were usually present. Of 2,583 individuals taken in the samples, 34 were of several families of parasitic wasps and 2,549 were ants. Whereas Formicidae are to be expected in tree-hole mold, they are never in overwhelming numbers unless an ant nest is involved. This was the case in sample No. 3 from Polk County, Florida, in which a grapefruit mold sample of 570 grams yielded 3,082 arthropods, of which 2,386 were *Monomorium floricola.* This latter figure included nine queens, 2,377 workers, of which many were callows, several larvae and many ant eggs. The effect of a large aggregation upon percentage distribution is illustrated once more. The remaining seventeen samples contained only 163 ants. Consequently this great local abundance of *M. floricola* was adjusted in Table II to bring the percentage figures into more realistic averages of formicids per kilogram of tree-hole mold.

Family distribution in Collembola

Collembolans and mites usually form the great majority of arthropods in any sample of prairie soil or sod, forest-floor litter, log mold or tree-hole mold. Numbers of Collembola may be prodigious locally (Park 1949).

Collembola and Acarina have been recognized as an important part of the soil and floor faunas by many investigators, in many parts of the world and in diverse habitats, *e.g.,* in grass tussocks near Oxford, England (Ford 1937, 1938); in pasture soil near Cambridge, England (Salt *et al.* 1948); in leaf- and log-mold of an Illinois deciduous forest floor (Lunn 1939); in leaf mold of a Panamanian rain forest (Williams 1941); soil of a cacao plantation and of a savannah in Trinidad (Strickland 1947). The earlier literature on soil and litter populations is cited in the bibliography of Fenton (1947).

In the 18 samples reviewed in this report, the Collembola were found in all samples, and made up some 27 per cent of the arthropods in the average kilogram of tree-hole mold. From Table I it will be noted that the springtails varied in their population density per kilogram from a low of 0.4 per cent to a high of 72.4 per cent. One conclusion seems trustworthy, that whereas collembolans may dominate certain types of forest and grassland biotopes on occasion, they very seldom outnumber the acarinids in tree-hole mold. Only in two samples out of 18 studied here, Nos. 3 and 4, both from Florida, did they make up more of the kilogram's total than did the mites.

Since the collembolans are important herbivores in the tree-hole food web, the families are analyzed by sample in Table III.

Of the three families represented, in terms of frequency, the Entomobryidae and Poduridae were almost the same, occurring in 17 and 16 of the 18 samples respectively, whereas the Sminthuridae were about half as frequent, occurring in only 8 samples. In terms of abundance of indi-

TABLE III. *Collembola in Tree Holes.*

Tree-hole Sample	Entomobryidae per kilogram	Poduridae per kilogram	Sminthuridae per kilogram
1	136	0	0
2	86	401	2
3	100	112	788
4	2,601	14	0
5	149	1	0
6	152	172	22
7	101	251	1
8	185	77	0
9	3	3	0
10	190	2	27
11	109	5	0
12	23	1	0
13	0	0	1
14	814	7	0
15	26	3	0
16	1,494	138	2
17	7	7	1
18	85	7	0
Totals	6,261	1,201	844
Averages for times collected	368	75	105
Averages for all samples	348	67	47

viduals, the Entomobryidae were by far the most numerous (Table III), *viz.*, five times as abundant as the Poduridae and more than seven times as abundant as the Sminthuridae.

It is of interest to note that in ten of the eighteen samples the Entomobryidae comprised 86% or more of the Collembola present, with the other two families absent or sparsely represented. In five samples, the Entomobryidae and Poduridae were relatively equal in numbers (samples No. 6, 7, 8, 9, and 17).

Family distribution in Coleoptera

As noted previously, the Coleoptera were one of three orders of arthropods that occurred in all 18 samples of tree-hole mold. In so far as this habitat niche is concerned, the beetles are the best known taxonomically. Fifty species of arthropods have been identified from these samples, and of this number thirty-six, or 72 per cent, are beetles. Family distribution is given in Table IV, with respect to adults, and Table V, with respect to larvae.

TABLE IV. *Families of Adult Coleoptera in Tree Holes.*

Family (adults)	Times collected in 18 samples of tree-hole mold	Total number collected in 18 kilogram-samples
Carabidae	7	16
Silphidae	2	3
Scydmaenidae	5	16
Ptiliidae	8	576
Staphylinidae	12	37
Pselaphidae	7	44
Histeridae	5	48
Murmidiidae	1	2
Cryptophagidae	3	7
Colydiidae	1	1
Cucujidae	1	1
Mycetophagidae	1	1
Lathridiidae	2	8
Corylophidae	2	3
Euglenidae	1	1
Dermestidae	1	1
Cisidae	3	351
Elateridae	1	1
Trogidae	1	1
Anthicidae	1	1
Tenebrionidae	2	3
Curculionidae	7	56

TABLE V. *Families of Larval Coleoptera in Tree Holes.*

Family (larvae)	Times collected in 18 samples of tree-hole mold	Total number collected in 18 kilogram-samples
Scydmaenidae	1	1
Staphylinidae	3	16
Pselaphidae	1	19
Histeridae	1	1
Dermestidae	1	1
Elateridae	13	71
Rhipiceridae	1	1
Cantharidae	1	1
Alleculidae	5	25
Tenebrionidae	5	32
Chrysomelidae	1	2
Unknowns	10	99

From this table it will be seen that there are six families of beetles that are in considerable abundance. These are the Ptiliidae, Staphylinidae, Pselaphidae, Histeridae, Cisidae, and Curculionidae.

The Ptiliidae are usually present in samples, and usually in abundance. There is one datum that suggests full-time residence of at least certain species in the habitat. On June 13, 1950, a ptiliid was found in the berlesate of sample No. 10 that had been killed while emerging from the pupal exuviae. This was a species of *Micridium*. Another pertinent datum is the presence of fungus spores in their gut. Since these minute beetles are usually present, often in relatively large numbers; since at least some species apparently pass their pupal stage in the habitat; and since they apparently feed, in part at least, on fungi—food stuff that is usually abundant in tree holes—it would seem safe to conclude that the ptiliids are normal tree-hole residents.

The Staphylinidae are one of the largest families of beetles known and it is not surprising that rove-beetles were found in twelve out of eighteen samples. It is thought that the family is primarily carnivorous, and there are relative myriads of mites, collembolans and small larvae to devour in the mold. Larvae of Staphylinidae were found in at least three samples (Nos. 2, 14, 16). The tree-hole habitat would seem to be a normal residence of certain species.

The Pselaphidae are relatively well known as tree-hole residents and have been discussed previously in this regard (Park, Auerbach, and Corley 1950). They occurred in the samples in about the same frequency as the ptiliids, and in about the same density as the staphylinids. The life history of Pselaphidae is virtually unknown (Park 1942, 1947b) but the larvae of two species have been illustrated and keyed out (Böving and Craighead 1931). These two are *Euplectus confluens* and *Batrisodes monstrosus*. As noted in the faunal checklist, both of these genera are reported from tree-hole mold, and one of the species as well, *i.e., Euplectus confluens confluens and Euplectus confluens iowensis.*

Euplectus confluens was collected from samples Nos. 2, 8, 11 and 16. From No. 16 also were taken 38 larvae that agree in all particulars with the description and illustration of the larva of this species as given by Böving and Craighead (1931). Since this was a two-kilogram sample, the population of the mold at the time of collection had a

density of 15 adults and 19 larvae per kilogram.[5] Park, Auerbach, and Corley (1950) found *Euplectus confluens* abundant in tree-hole molds, especially of beech trees, and this species composed 80 per cent of the pselaphids collected.

Pselaphids are known to feed on mites and other small arthropods (*cf.* Park 1947a, 1947b), and since these beetles are relatively abundant in the habitat, and since what appear to be their larvae have been collected from a sample, we may conclude that these beetles also are normal residents of tree holes.

The fourth abundant family, the Histeridae, was taken in five of eighteen tree holes, and in slightly higher numbers than the pselaphids. The histerids are probably predaceous. Histerid larvae, probably of *Hololepta,* were collected from sample No. 2. As with ptiliids, staphylinids and pselaphids, these data on abundance, food habits not at variance with the known foods available, and presence of immature stages in the substrate, suggest that the histerids are normal tree-hole residents.

The Cisidae are herbivores, feeding on fungi primarily so that their food requirements are abundantly supplied both within the tree hole, and from the fungus conks that are often found on the tree trunks. Although cisids were taken only in three samples, they may occur in great numbers and in the present report they were represented by three genera and 351 individuals. The majority of these were in one sample, No. 6, in which *Ceracis sallei* was represented by 348 individuals. Cisid larvae were not found in the samples studied, and it may be that these beetles should be regarded as normal residents of the fungus conk biotope rather than the tree-hole biotope, although both microseres may commonly merge in the decaying log microsere.

The last family that was present in numbers is the Curculionidae. These weevils vie with the staphylinids as the largest family of beetles, and since many species have their larval stages in tree wood and since the family is well known for its herbivorous habits, it is not surprising that weevils should have occurred in seven of eighteen samples of mold, and were relatively abundant. The eighteen kilogram-samples reported yielded 56 individuals. No curculionid larvae were taken in the mold.

There are eleven families listed in Table V.

[5] In view of the lack of information on the life history of Pselaphidae, the regular berlesing of tree-hole mold through the several seasons is a promising research lead. The authors are at present involved with such a program, and if pselaphid larvae appear, these will be allowed to fall into prepared petri-dish containers so that the subsequent history of the larvae, if any, may be studied.

TABLE VI. *Species of Coleoptera in Tree Holes.*

Determination	Tree-Hole Numbers (Table I)
Carabidae	
Agonoderus pallipes (Fabricius)	10, 12
Calosoma scrutator (Fabricius)	11
Tachymenis flavicauda (Say)	2, 4, 11
Silphidae	
Catops terminans (LeConte)	15
Ptomaphagus pusio LeConte	18
Scydmaenidae	
Connophron debilitans Casey	12, 16
Staphylinidae	
Thoracophorus costalis Er.	2, 3, 11
Xantholinus gularis LeConte	18
Xantholinus near *sanguinipennis* LeC.	2
Pselaphidae	
Batrisodes globosus (LeConte)	7, 9
Euplectus confluens LeConte	8, 11, 16 (adults and larvae)
Euplectus iowensis Casey	2
Euplectus interruptus LeConte	18
Thesium cavifrons (LeConte)	16
Histeridae	
Bacanius misellus LeConte	4
Carcinops 14-striata Steph.	2
Dendrophilus opacus Ross	2
Dendrophilus punctatus Hbst.	12
Dendrophilus zavierae Lewis	2, 12
Epirus pulicarius Erichson	12
Isolomalus seeversi Wenzel	2, 10, 12
Xestipyge conjunctum (Say)	2
Cucujidae	
Laemophloeus biguttatus Say	6
Cryptophagidae	
Cryptophilus integer (Heer)	8
Loberus impressus LeConte	18
Colydiidae	
Cerylon castaneus Say	18
Dermestidae	
Anthrenus museorum (Linnaeus)	16 (adults and larvae)
Mycetophagidae	
Mycetophagus flexuosus Say	5
Lathridiidae	
Melophthalmus parviceps LeConte	14
Cisidae	
Ceracis sallei Mellie	6
Cis creberrima Mellie?	12
Rhipiceridae	
Zenoa picea (Beauv.)	12 (larvae)
Elateridae	
Aeolus dorsalis (Say)	12
Alleculidae	
Capnochroa fuliginosa (Melsh.)	2, 9, 12, 15, 16 (larvae)
Tenebrionidae	
Tenebrio picipes Hbst.	1, 2, 16, 17 (larvae); 12 (adults and larvae)
Platydema ruficorne Sturm.	12

There were beetle larvae present in all the berlesates with the exception of two, Nos. 3 and 13. The total number of larvae collected was 269, *viz.,* 20.7 larvae per kilogram for the sixteen samples in which they occurred, or 14.9 larvae per kilogram for an average of all samples studied. Of the 22 families represented by adults, 7 families were also present as larvae (Scydmaenidae, Staphylinidae, Pselaphidae, Histeridae, Dermestidae, Elateridae and Tenebrionidae). This is a fairly high proportion, and considering the small number of samples and the relative state of larval beetle taxonomy, this is a satisfactory situation.

Of the larvae identified, it will be noted that the Elateridae outweigh any other family both in occurrence in number of samples and in kilogram-sample total. To the six families already discussed should be added Elateridae, and probably Alleculidae and Tenebrionidae as tree-hole residents. These latter three would appear not to be full-time residents, but to have their larval period normally passed in tree-hole mold.

Direct attention should be given to the relatively high proportion of beetles identified to species. Such determinations to species in connection with habitat niches having definite localities may be of assistance to others interested in this kind of program.

Of interest in Table VI is the relatively high number of species that occur in more than one tree hole. There are ten of the "repeaters," or nearly a third of the species, in this category. Considering that only eighteen samples were berlesed, and that so many species remain unidentified, this is a gratifying proportion. Two genera, the pselaphid *Euplectus* and the histerid *Dendrophilus,* each have three taxonomically distinct populations involved in the tree-hole biocoenosis, and both genera would appear to be well adjusted to this habitat.

Adults and larvae of three species were collected from the same tree holes, *e.g., Euplectus confluens, Anthrenus museorum,* and *Tenebrio picipes.*

Two species, *Capnochroa fuliginosa* and *Tenebrio picipes,* were particularly common in the larval stage, being collected in five tree holes each.

The Microclimate of Tree Holes

The forest community modifies local weather conditions to form its own climate. This is especially true during the period of foliation. This general process may be regarded as unconscious control by organisms of their environment, and is one of the biotic manifestations of a major community.

This control is especially exerted by the highest stratum, the canopy, and from ecotone inward, and from canopy downward, each stratum tends to reinforce this progressive modification of physical influences. Consequently there is less air movement within a forest than outside it. By day the forest is darker, cooler, has a higher relative humidity and a lower rate of evaporation than extra-forest areas under normal circumstances. In successive days the forest is relatively darker, cooler and moister by night than by day.

Just as the forest has its own climate, so the tree hole has its own microclimate. Protected by a more or less intact wall of living and/or dead wood except for the orifice or orifices, the relatively small volume of the tree-hole habitat has a microclimate that is relatively less variable than that of extra-tree-hole areas, both from day to day and day to night.

There are a few data on the microclimate of tree holes. A small amount of information was collected on one tree hole under study in this report. This (No. 15) was in a living wild black cherry, at Turkey Run State Park, Parke County, Indiana, and had an irregularly fusiform orifice fourteen inches high and six inches wide, with the orifice four feet from the forest floor. The tree hole was filled with soft mold that filled the cavity flush with the orifice lip. This tree hole had an inside diameter of ten inches, and above the orifice extended upward for eighteen inches. Readings of physical influences were begun at 10:00 P.M. (C.S.T.), June 7, 1950, and continued to 6:00 A.M., June 9. These readings included the temperature of mold, tree-hole air, air outside of the tree at four feet from the floor; relative humidity of the tree-hole air, and of the air outside the tree; light intensity of the tree-hole cavity, and of the forest floor, and in the open sun near the tree hole. These data are summarized in Table VII.

Table VII. *Microclimate of a Tree Hole.*

Date and Time (C.S.T.)	Temperature (°F)			Relative Humidity (%)		Light Intensity (foot candles)		
	Tree-hole mold	Tree-hole air	Air by tree hole	Tree-hole air	Air by tree hole	Tree hole	Forest floor	Open sun
7. VI. 50								
10:00 PM	67.0	....	67.0	81	88	0	0	0
12:00 M	66.0	....	65.0	81	88	0	0	0
8. VI. 50								
2:00 AM	66.0	....	64.0	85	90	0	0	0
4:00 AM	65.5	....	62.0	100	98	0	0	0
6:00 AM	65.0	....	65.0	93	90	1	14	1,700
9:30 AM	68.0	73.0	78.0	79	68	10	100	9,500
12:00 N	69.0	76.0	82.0	77	66	10	120	12,400
3:00 PM	70.0	77.0	82.0	66	66	6	80	8,800
5:30 PM	70.5	76.0	79.0	76	73	1	22	2,600
7:30 PM	70.5	74.0	74.5	82	85	0	0	4
10:00 PM	70.0	72.0	73.0	83	87	0	0	0
12:00 M	70.0	71.0	69.5	96	89	0	0	0
9. VI. 50								
2:00 AM	70.0	70.0	68.0	94	89	0	0	0
4:00 AM	70.0	70.0	68.5	100	95	0	0	0
6:00 AM	70.0	71.0	71.0	96	96	2	20	1,100

From these data it is clearly demonstrated that the tree-hole environment is less variable with respect to temperature, relative humidity, and light intensity than is the forest environment as a whole. Such a situation would have been predicted in view of the protected and restricted nature of the tree hole, and needs no further comment. Such mediation of the physical influences may play an important rôle in the microcosm

under study, *e.g.*, in the conservation of moisture content of the tree-hole mold.

General Discussion

The tree hole is a fascinating habitat niche. As a consequence of its relatively restricted volume and relative isolation it lends itself to quantitative biological study. Such studies could involve mycology, protozoölogy, nematology; and entomology, in the broadest sense of the term to embrace certain aspects of parasitology as well as acarology.

Certain general principles and facts are known concerning the tree-hole community, but many more things are unknown. In a general way, it may be said that the tree hole has a large and diversified arthropod fauna. Of this fauna, the Acarina are the most numerous order. In addition to the mites, Collembola and Coleoptera are almost always present, frequently in numbers. The Entomobryidae among collembolans, and Ptiliidae, Staphylinidae, Pselaphidae, Histeridae, Cisidae, Curculionidae, and Elateridae are the most abundant beetle families studied in the present report.

The tree hole has its own microclimate. This is more stable than extra-tree-hole microclimates. By day the tree hole is darker, more humid, and cooler than the surrounding forest. The substrate, a well-worked log mold plus fungus hyphae and chitin fragments, is characteristically moist. Water content is relatively high for most of those tree holes with abundant arthropods, between 55 and 75 per cent free water by weight.

The tree-hole microsere involves three alternative routes, *e.g.*, the living tree seals off the cavity, or the cavity is seasonally or annually full of water and parallels the developmental history of a pond, or the tree hole is occupied by a terrestrial biota. This microsere is integrated with the fungus-conk microsere, and with the decaying-log microsere. Hence the tree-hole history does not involve a climax stage, but is a part of that of the forest community as a whole.

The tree hole has its own biota. This latter is involved in the general energetics of the whole community metabolism, but on a smaller scale. There is a definite food-web. This food-web contains herbivores, predators, parasites, and very probably heterotrophic bacteria and fungi and autotrophic bacteria. The initial trophic level, that of the photosynthetic plants, is typically absent.[6] In this respect the tree hole resembles the cave community.

In the case of the cave community the initial energetic input is from guano and/or vernal flooding. In the case of the tree hole community the initial input is supplied by the metabolic end-products of the living tree in which the habitat develops. In a peculiar sense, the higher trophic levels are inhabiting the first level. In this sense the tree hole resembles the entoparasite, or in a more exact way, the dermatocolous larvae of botflies (Cuterebridae).

The tree-hole fauna has been shown to follow the principle of the pyramid of numbers (*cf.* Fig. 3, Park, Auerbach and Corley, 1950). Although the herbivore-to-predator ratio varies from sample to sample of tree-hole mold, the herbivores are relatively numerous as would be expected. In the eighteen tree holes reported on here the ratio of herbivores to predators varied from 160/1 to 9/1. In the initial report(Park, Auerbach, and Corley 1950), less attention was paid to quantitative aspects of the whole fauna, but the ratios varied from 126/1 to 8/1. In all such ratios an element of inaccuracy is inescapable. This is caused by lack of definite information on the food habits of some of the organisms. These latter cannot be used to bolster this ratio, and include numerous larvae of unidentified beetles and fly larvae and certain groups of mites. Again, these ratios refer to the arthropods only. Even within such restrictions there are difficulties. For example, small predators may not have the same effect on herbivore consumption as do relatively large predators, and with more study the H/P ratio may have to be factored.

Groups that were regarded as herbivorous contained those feeding on the log-mold substrate as well as those feeding upon fungi in the mold or on the cavity walls. Among these herbivores can be listed the oribatoid mites, the collembolans, thrips, corrodentids, beetles of Chrysomelidae, Corylophidae, Ptiliidae, Tenebrionidae, Elateridae and Curculionidae, and millipeds.

The several predator grades included trombid mites, centipedes, pseudoscorpions, spiders, and beetles of Scydmaenidae, Pselaphidae and at least certain Staphylinidae.

In addition the picture is complicated by the stray predator, the effect of which cannot be estimated in the present state of our ignorance. For example, tree hole No. 11 contained an individual of the large, nocturnal, predaceous carabid, *Calosoma scrutator*. This species is known to climb trees in search of caterpillars (Balduf 1935).

Below the carnivore level of predators and parasites the available information is even less. There

[6] Stray grasses or herbaceous plants, epiphytes, and vines may inhabit the orifice and send roots into the subjacent mold or partially block the orifice. This is uncommon. Such plants do not habitually grow on the mold in the dark interior; they are adventitious in so far as the tree-hole biocoenosis is concerned.

are no data on the presence and activities of the heterotrophic bacteria and fungi as they relate specifically to tree-hole mold, nor on the autotrophic bacteria. The general rôles of these last two trophic levels have been discussed in Allee *et al.* (1949, pp. 495-528).

These two trophic levels undoubtedly function in the tree-hole mold. The organic products are there for heterotrophic consumption and reorganization. Cellulose from the tree is obviously present, and in quantity. This should yield glucose, and possibly fatty acids and nitrogen. Tannin is probably present, especially if the tree hole is in chestnut or if the bark of oaks and hemlock are involved. This should yield gallic acid, among other things, if the trophic level can supply a tannase.

For example, certain fungi of the genera *Aspergillus* and *Penicillium* elaborate tannase and break down tannin into gallic acid if oxygen and 10 per cent glucose are present (Foster 1949). Glucose would be a product of decomposition of cellulose, and oxygen is available in the tree hole.

In addition to cellulose, there is another polysaccharide available in the mold. This is chitin. Even casual inspection of a pinch of tree-hole mold reveals chitin fragments—reminders of the large arthropod population inhabiting the biotope. Chitin is also available in the dead mycelium of numerous fungi, *e.g.,* many of the Eumycetes, and some of these may be involved in tree-hole energetics.

Hydrolysis of chitin yields glucosamine if insects and crustaceans are involved (Harrow 1950), or glucosamine and acetic acid if fungus mycelia are involved (Foster 1949). Glucosamine is a breakdown product of arthropod chitin in general, according to Richards (1951). Hence relatively large amounts of chitin are available for heterotrophic action through the years in which the tree hole enlarges and passes through the microseral stages.

In addition to these three possible primary tree-hole substances (cellulose, tannin, and chitin), there are the continual additions of faeces and the dead bodies of the arthropods. Little data are available on either. Juritz (1920) analyzed the faeces of the caterpillar, *Antheraea cytherea,* and found that their droppings compared favorably with dung of grassland mammals in the relative proportions of nitrogen, lime, and phosphoric acid.

Bacterial decomposition of the proteins of dead arthropods should follow the same general lines as similar decomposition of putrefying vertebrate flesh. Thus (Harrow 1950) decarboxylation of lycine produces cadaverine, and that of arginine produces putrescine.

From such possibilities there emerges the probability that, with the exception of green plants, the tree-hole food-web contains all the trophic levels of the whole forest, and exhibits a complete though restricted niche metabolism.

To paraphrase Causey (1952), the tree-hole arthropods "live out their little hours" in the rich mold, mutually molesting and being molested by one another.

Summary

Samples of mold from eighteen tree holes were weighed, the contained arthropods extracted by Berlese funnels, and the mold samples reweighed to estimate the free water content of the tree-hole substrate.

One sample contained so many empty tests of a rhizopod protozoan that specially weighed small samples were examined directly and the tests counted. The rhizopod was *Difflugia arcula* Leidy. There were 174 tests in 33.4 milligrams of mold. Assuming random distribution, this would give an estimated density of 1,910 tests per gram. Possible rhizopod colonization of certain kinds of tree holes is discussed.

A taxonomic census of the eighteen tree holes yielded 23 orders, 68 families, 93 genera, and 51 identified species of arthropods.

Factors that may affect tree-hole population density include new generations, ants, nesting mammals, and water content of the substrate. These influences are discussed.

The 23 arthropod orders are compared as between the 18 tree holes for percentage frequency, average population density per kilogram of wet mold, and average percentage of total population of sample. The average kilogram was found to contain 2,477 arthropods. Several orders are discussed in terms of the tree hole complex. These include Acarina, Coleoptera (larvae and adults), Collembola, Diptera, Heteroptera, Homoptera, Hymenoptera (chiefly Formicidae), Lepidoptera, Phalangida, and Orthoptera.

Acarina and Collembola were most numerous, comprising 61 per cent and 27 per cent of the average kilogram respectively.

Three orders, Acarina, Collembola, and Coleoptera had the highest percentage frequency, being found in 100 per cent of the samples examined.

Six families of beetles (Ptiliidae, Staphylinidae, Pselaphidae, Histeridae, Cisidae, and Curculionidae) were especially abundant. These six families, three families of Collembola, and Formicidae are discussed in more detail.

The microclimate of one tree hole was studied. Air and substrate temperatures, relative humidity, and light intensity were measured in the tree hole,

and compared with the same influences operating just outside of the tree hole, over a period of 32 consecutive hours in June, 1950.

The tree hole habitat is discussed in general terms, with emphasis on trophic levels involved and the possibility of the requisite biochemical agencies being present to render the habitat efficient biologically.

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SPACING IN PLANT POPULATIONS

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Introduction

Considerable attention has been devoted in the past few years to the distribution of the number of plants of a given species that occur in a quadrat thrown at random on to a large area. Archibald (1948) and Thomas (1949), among others, have discussed this problem and have demonstrated that the Poisson limit to the binomial, which should hold if the plants are distributed at random, is untenable for nearly all the plant populations met with in practice. In the place of Poisson's limit, various alternative series suggested by Neyman (1939), Thomas (1949), and Fisher (1941) have been tried but these series often suffer from the difficulty of the practical interpretation of their parameters. Evans (1953) has examined three

alternative series in some detail and concludes that Neyman's series of Type A is the most useful for plant populations.

For a long time, investigations have been made of the numbers of accidents occurring in successive equal intervals of time. More recently, the intervals between successive accidents have been used by Greenwood (1946), Moran (1951), and Maguire *et al.* (1952) to examine whether the accidents are occurring randomly. This suggests that instead of sampling plant commonwealths by quadrats, which corresponds to counting the number of accidents occurring in fixed intervals of time, an examination should be made of the spacing between plants of a certain species in the commonwealth. In this paper it is proposed to discuss the following problem. A point is selected at random on a large area and the distance to the nearest plant measured. The process is repeated and it is desired to examine the distribution of this distance under the assumption that the plants are distributed at random in the commonwealth and alternatively that there is some form of clumping present.

The selection of a point at random on a given area is probably easier to do in practice than the selection of a plant at random. This follows from the fact that for the latter every plant must first be enumerated and then a drawing made by means of random number or a similar device. To select a point at random there are a number of possible ways. A common method is to divide the field up into a large number of equal areas and to select one of these by means of random numbers. In this small area, usually a square or similar convenient shape, two numbers are selected from random numbers and are taken as the two coordinates of the point in the square.

Distribution of Distance

Let the mean density of plants per unit area be D and the plants be distributed at random over the area. This assumption is implicit both for Poisson's distribution and the work that follows in this and the two succeeding sections. This may mean that the methods are of greatest use in the case of relatively low densities when Poisson's law often holds most closely. We first find the probability that the nearest plant from a point chosen at random lies in a thin circular annulus or ring. This annulus is the area contained between two concentric circles having radii r and $r + \delta r$ respectively where δr is small compared with r. Thus, the nearest plant will be between r and $r + \delta r$ distant from the point selected at random. To find this probability, we take the product of the probability that no plants fall in a circle of radius r and the probability that one or more plants fall in the annulus. The first probability is approximately

$$e^{-\pi r^2 D}$$

since $\pi r^2 D$ is the mean number of plants expected in the circle and from a consideration of the Poisson distribution, the probability of no plants being present in the area is the first term of a Poisson series with parameter equal to the mean or $\pi r^2 D$. Similarly, the probability of one or more plants being in the annulus is

$$1 - e^{-2\pi r D\, \delta r}$$

and if we neglect powers of δr higher than the first as being negligible, this latter probability is equal to

$$1 - (1 - 2\pi r D\, \delta r) \text{ or } 2\pi r D\, \delta r$$

Hence the required probability is

$$2\pi r D e^{-\pi r^2 D}\ \delta r$$

If $p(r)$ be the elementary probability law of r, the distance of a point selected at random to the nearest plant, that is to say that the probability that r lies between a and b is given by

$$\int_a^b p(r)\, dr$$

then

$$p(r) = 2\pi r D e^{-\pi r^2 D} \qquad (1)$$

By a simple transformation of variables, we obtain the elementary probability law of $\omega = r^2$ as

$$p(\omega) = \pi D e^{-\pi D \omega} \qquad (2)^1$$

It follows from (2) that the quantity $2\pi D\omega$ is distributed as the well known function χ^2 with 2 degrees of freedom.

Further, if $\tilde{\omega}$ is the mean of n independent such distances then it can easily be shown that

$$p(\tilde{\omega}) = \frac{(n\pi D)^n (\tilde{\omega})^{n-1} e^{-n\pi D\tilde{\omega}}}{(n-1)!} \qquad (3)$$

The mean and standard deviation of $\tilde{\omega}$ are $(\pi D)^{-1}$ and $(\pi D\sqrt{n})^{-1}$ respectively and hence as n gets larger the standard deviation decreases From (3) it also follows that the quantity $2n\pi D\tilde{\omega}$ is distributed once again as a χ^2 distribution only this time with $2n$ degrees of freedom.

It is of interest to note that a further extension is possible to three dimensions. If points occur randomly in space with a mean density of D per unit volume and an origin is selected at random then the distribution of v, the cube of the distance from the origin to the nearest point is that of a χ^2 distribution with a scale alteration. In fact, the

[1] Equation (2) was recently given by J. G. Skellam, Biometrika 39: 349.

quantity $\frac{8}{3}\pi Dv$ is distributed as χ^2 with 2 degrees of freedom.

Estimation of Density

The results just obtained show that a variety of problems connected with the spacing of plants in a community may be successfully tackled by means of the χ^2 distribution which has been extensively tabled and whose properties have been investigated in some detail. For example, suppose that it is desired to estimate D, the density of plants per unit area. Since the distribution of $\tilde{\omega}$ has, from (3) a mean of $(\pi D)^{-1}$ we would expect $(\pi\tilde{\omega})^{-1}$ to be an estimator of D. In fact, it is an estimator, although a biased one. From (3) we have

$$E\left(\frac{1}{\pi\tilde{\omega}}\right) = \int_0^\infty \frac{1}{\pi\tilde{\omega}} \cdot \frac{(n\pi D)^n (\tilde{\omega})^{n-1} e^{-n\pi D\tilde{\omega}}}{(n-1)!} d\tilde{\omega}$$

where E is the symbol to denote the mean value in repeated sampling or expectation. Putting

$$n\pi D\tilde{\omega} = u$$

this reduces to

$$D \int_0^\infty \frac{n}{(n-1)!} u^{n-2} e^{-u}\, du = \frac{n}{n-1} D$$

Hence

$$E\left(\frac{n-1}{n} \cdot \frac{1}{\pi\tilde{\omega}}\right) = D$$

By similar reasoning, we may show that

$$E\left(\frac{n-1}{n} \cdot \frac{1}{\pi\tilde{\omega}}\right)^2 = D^2 \frac{n-1}{n-2}$$

and hence if

$$v = \frac{n-1}{n} \cdot \frac{1}{\pi\tilde{\omega}} = c/\tilde{\omega} \qquad (4)$$

then the variance of v is

$$\sigma_v^2 = D^2/(n-2) \qquad (5)$$

In practice we would have to substitute for D in (5) our estimate of D obtained from (4) so that we would have

$$s_v = \frac{n-1}{n} \cdot \frac{1}{\pi\tilde{\omega}} \cdot \frac{1}{\sqrt{n-2}} = k/\tilde{\omega} \qquad (6)$$

where

$$k = (n-1)/n\pi\sqrt{n-2} \qquad (7)$$

The values of c and k for various n are given in Table I. The value of c tends to the limit of $0 \cdot 3183$ as n gets large, whereas the value of k tends to zero. A comparison may be made of the

Table I. *Values of c and k for various n*

n	5	10	15	20	30	40	50	100	∞
c	.2546	.2865	.2971	.3024	.3077	.3103	.3119	.3151	.3183
k	.1470	.1013	.0824	.0713	.0581	.0503	.0450	.0318	.0

accuracy of estimating D by this method with the accuracy of estimating D by the more usual method of quadrat sampling. Suppose the size of quadrat is unity and it is thrown m times on to an area in which the average density of plants per unit area is D. If x be the mean number of plants counted per quadrat, then it is known that provided Poisson's limit to the binomial holds then

$$E(x) = D \qquad (8)$$

and

$$\sigma_x^2 = D/m \qquad (9)$$

Comparing (8) with (5) we see that the ratio

$$\frac{\sigma_v}{\sigma_x} = \sqrt{\frac{Dm}{n-2}} \qquad (10)$$

and thus depends on the three quantities D, m, and n. A few specimen values of the function σ_v/σ_x are given in Table II for some selected values of the variables D, m, and n. It will be noticed that for very low values of D, the method based on spacing is very much more accurate for the same value of m and n than the method based on quadrat sampling. With high values of D, the reverse is the case. When D is equal to unity, the two methods give about the same accuracy of estimate. From the table, we can also see that with, for example, $D = 0 \cdot 1$ a value of n equal to 10 gives an estimate of D with a standard error some 20% below one based on a value of m equal to 50, that is five times as many observations. Hence for very low densities, the spacing method would seem to be preferable although it is necessary, before making a final decision in any particular case, to weigh up the relative ease with which the two methods may be carried out. It must be borne in mind that these calculations are based on a quadrat of unit area or alternatively we are estimating the mean number of plants per quadrat over the whole area.

Comparison of Densities

The χ^2 tables may be used to provide a confidence interval for the unknown value of D. Thus if $\chi^2_{f,\alpha}$ is the value of χ^2 with f degrees of freedom such that the probability of its being exceeded

TABLE II. *Values of σ_v/σ_ω or relative efficiencies of quadrat and spacing methods*

	$D=0.1$			$D=0.5$			$D=1$			$D=2$			$D=3$		
m	10	20	50	10	20	50	10	20	50	10	20	50	10	20	50
10	.35	.50	.79	.78	1.12	1.77	1.11	1.58	2.50	1.57	2.24	3.53	1.92	2.74	4.33
n 20	.23	.33	.53	.51	.74	1.19	.74	1.05	1.67	1.03	1.48	2.37	1.26	1.81	2.90
50	.14	.20	.31	.31	.45	.69	.46	.65	1.02	.63	.89	1.39	.77	1.10	1.70

by chance is α then there is a probability of $(1-\alpha)$ that

$$\chi^2\,2n, 1-\tfrac{1}{2}\alpha \leq 2n\pi D\tilde{\omega} \leq \chi^2\,2n, \tfrac{1}{2}\alpha \qquad (11)$$

or that

$$\chi^2\,2n, 1-\tfrac{1}{2}\alpha \,/\, 2n\pi\tilde{\omega} \leq D \leq \chi^2\,2n, \tfrac{1}{2}\alpha \,/\, 2n\pi\tilde{\omega}$$

This procedure may be used quickly with the aid of tables of the percentage points of the χ^2 distribution. For example, suppose that after 25 random points had been chosen the mean value of $\omega = r^2$ was found to be $\tilde{\omega} = 0 \cdot 81$. The upper and lower 2.5% points of χ^2 with 50 degrees of freedom are 71.4202 and 32.3574 respectively. Hence we have

$$\frac{32.3574}{50\pi(0.81)} \leq D \leq \frac{71.4202}{50\pi(0.81)}$$

or $$0.2540 \leq D \; 0.5613$$

with a probability of 0.95 that the inequality does cover the true value of D. If we have two independent estimates of χ^2 with f_1 and f_2 degrees of freedom respectively then the variance ratio F is defined as

$$F = \frac{\chi^2_1}{f_1} \Big/ \frac{\chi^2_2}{f_2}$$

where χ^2_1 and χ^2_2 are the two values of χ^2 and F has f_1 and f_2 degrees of freedom. From the results obtained earlier, we see that if $\tilde{\omega}_1$ is the mean of n_1 squared distances from random points and $\tilde{\omega}_2$ is the mean of n_2 independent squared distances to the nearest plant, then $D_1\tilde{\omega}_1/(D_2\tilde{\omega}_2)$ will be distributed as an F ratio with degrees of freedom $f_1 = 2n_1$ and $f_2 = 2n_2$.

This ratio can clearly be used to test whether the density of plants is the same in two populations, it being assumed that the plants are distributed at random in both cases. For example, on one field it was found that a particular species gave a value of $\tilde{\omega}$ equal to 1.22 based on 60 distances. On another field with the same species, a value of 0.93 was found for $\tilde{\omega}$ based on 30 distances. The ratio $1.22/0.93 = 1.31$ and if the two densities are the same than this ratio will be distributed as an F ratio. From the tables of F given by Merrington and Thompson (1943) with $f_1 = 120$ and $f_2 = 60$ it is clear that there is no evidence from these data alone as to a difference in the densities of plants in the two fields.

TEST OF RANDOMNESS

We turn now to the problem of deciding, on the basis of the distances from points to the nearest plant, whether the plants in a large area are in fact distributed at random or not. It may be that the density of plants is varying slowly over the field due to such things as patches of fertile soil so that the density is dependent on the position in the field from which the samples are chosen. To test whether this is so or not, a test of homogeneity may be carried out. The field of area is subdivided into k units and in each unit h points are selected at random and the distances measured to the nearest plants. If $\tilde{\omega}_i$ is the mean of the squares of these distances in the i th unit then the test criterion to be calculated is

$$M = 2hk \left\{ \log_e \frac{1}{k} \sum_{i=1}^{k} \tilde{\omega}_i - \frac{1}{k} \sum_{i=1}^{k} \log_e \tilde{\omega}_i \right\} \qquad (12)$$

Tables have been computed by Thompson & Merrington (1946) giving the 5% and 1% significant points for M. If our observed results established significance, we would reject the idea that the density of plants was remaining constant in favor of the alternative that the density varies over the field. The test is extremely useful in that the density of plants, or an estimate of it, is not required. The test, however, suffers because the manner in which the field is sub-divided into k units is only one of an infinity of possible ways that such a sub-division could be made. A different method of subdivision could quite well produce a very different value for M.

A different form of alternative would be that the plants tended to occur in clumps and thus the distribution based on randomness does not hold even over a small area of the ground. Suppose that instead of ω having a distribution as given in (2) it has the distribution

$$p_1(\omega) = (\pi D q)^q \omega^{q-1} e^{-\pi D q \omega} / \Gamma(q) \qquad (13)$$

which is one of Pearson's Type III distributions. If we now take k points at random and find ω in each case then the likelihood ratio test that the distribution of ω is given by (2) against the alternative that the distribution is of the form defined by (13) is the criterion M defined in (12) above with h equal to unity. This test is derived by Moran (1951) in connection with the intervals between events and before it can be selected as a valid test, it is necessary to know from experimental evidence whether (13) is a valid description of the distribution of ω when clumping is present. It will be noticed that the mean of (13) is $(\pi D)^{-1}$ as was the mean of (2). Hence it is assumed that the clumping is such that the mean of the squared distances to the nearest plants from points chosen at random is unchanged, which is probably unlikely to the be the actual case in practice.

Dice (1952) has made some observations on the spacing of four species in a plant community, considering one species at a time. He selects plants at random and using these plants as centers of origin he measures the distance to the nearest plant of the same species in each of the six sextants surrounding the plant. It can be shown that the mean of his distributions are less than would be expected if the plants were distributed at random. It is difficult to assess the form of the distribution when clumping is present since by taking measurements in the six sextants, he obtains six values that are not independent of one another. However his histograms suggest that if there is clumping present, then by selecting a plant at random and measuring the distance to the nearest plant we obtain a distribution which has a lower mean than it would if the plants were spaced at random.

The foregoing suggests a different form of criterion that might be used to test for the presence of clumping or otherwise. If the plants are distributed at random and we select a plant at random, then the distribution of the distance from that plant to the nearest plant is the same as the distribution of the distance from a point selected at random to the nearest plant. Thus, under the hypothesis of randomness the ratio $\tilde{\omega}_1/\tilde{\omega}_2$ is distributed as an F ratio with $f_1 = 2n_1$ and $f_2 = 2n_2$ degrees of freedom where $\tilde{\omega}_1$ is the mean of n_1 squared distances from points chosen at random to the nearest plant and $\tilde{\omega}_2$ is the mean of n_2 squared distances from plants chosen at random to the nearest neighboring plant. Under the alternative hypothesis that there is clumping present, we would expect this ratio to be too large since the numerator would tend to be greater than under randomness and the denominator smaller. Thus, this test could be used to detect clumping of the form that has been envisaged above. It does mean, of course, that each plant of the particular species being considered must be enumerated in order that a plant may be selected at random and this may be an extremely tedious procedure.

If the density of plants is known from some subsidiary analysis, it is quite possible to utilize equation (3) direct. The quantity $2n\pi D\tilde{\omega}$ should be distributed as a χ^2 with $2n$ degrees of freedom. If clumping is present, our values of ω will tend to be too big and hence using the upper percentage levels of χ^2, we may easily test whether there is clumping or not. For example, suppose $D = 1 \cdot 12$, $n = 20$ and $\tilde{\omega}$ is found to be $0 \cdot 524$. Then $2n\pi D\tilde{\omega}$ is equal to $73 \cdot 75$ and as the upper 1% point of χ^2 with 40 degrees of freedom is $63 \cdot 69$, our observed value is indicative of considerable departure from randomness and hence clumping in some form is present.

Conclusion and Summary

The problem of examining randomness in plant populations has assumed considerable importance in recent years. This is because so many practical methods of plant sampling assume randomness that it is essential to be able to see whether this assumption is justified or not. Nearly all the previous work on this problem has utilized the methods of quadrat sampling. We have seen here how numerical studies based on the spacing between the plants in a large area can be utilized as an alternative method for investigating randomness. The various theoretical results derived are all fairly simple and are based on well known statistical functions. Further, the fields of application of these results are clearly very wide.

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TUBERCULOSIS AMONG WILD VOLES: WITH A DISCUSSION OF OTHER PATHOLOGICAL CONDITIONS AMONG CERTAIN MAMMALS AND BIRDS

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1. INTRODUCTION

Populations of the field vole (*Microtus agrestis*) often fluctuate between extremes of abundance and scarcity, and when the present study was begun it was thought that infectious disease might cause the recurrent high mortality about every 4 years. This paper describes part of the work carried out by Dr. A. Q. Wells and myself upon voles at Lake Vyrnwy, Montgomeryshire during 1936-9. The area and the field evidence are described by Chitty (1952) and the pathological discoveries by Wells (1937, 1946); here we are concerned with the correlation of these two aspects. Tuberculosis (*Mycobacterium tuberculosis*) was the only recognizable infectious disease and as will be shown it did not account for the population changes.

Such evidence does not, of course, prove that other diseases were absent, nor does it prove that disease is unable to control the numbers of other populations. At the same time it is clear that the mere association of disease with population decrease is not sufficient to prove a causal connection. Therefore, after the incidence of tuberculosis has been discussed, certain other studies are reexamined in order to show that deductions that epizootics control animal numbers are not always valid.

Elsewhere I have suggested that at times of periodic decrease certain generations of voles die because they are "abnormal from birth and thus more susceptible to various mortality factors" (Chitty 1952). According to this view diseases of one sort or another are part of a variable group of environmental hazards to which populations are especially vulnerable at certain stages of abundance. This unifying concept of a predisposing condition may also prove helpful in interpreting mortality among game birds.

The principal study areas are shown in Figure 1. Work was at first confined to Glasgwm (A1) where there were up to 300 voles per acre during 1936 and 1937. In the spring of 1938 these voles became very scarce. Elsewhere (except in area E) voles remained abundant until 1939, when there was great scarcity everywhere.

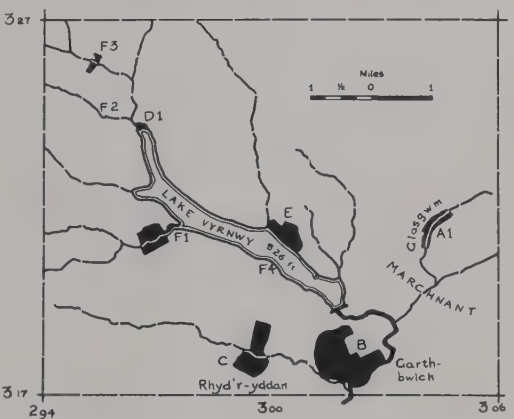

FIG. 1. Sketch map of the Lake Vyrnwy area based on the 1-in. Ordnance Survey map (1947) No. 117. 1-km. coordinates of the National Grid are shown by breaks across the frame and the principal streams. Black areas are conifer plantations occupied by field voles. During 1938 animals were scarce in the Marchnant watershed and at E, but remained abundant elsewhere until the spring of 1939. (Few animals were trapped at F1, as much of the habitat was unsuitable.)

2. METHODS

Our studies owe much to the work carried out by various colleagues in the previous ten years (Elton 1942). At first we followed the same procedure of bringing live animals into the laboratory and waiting for them to develop symptoms; later on most of our samples consisted of animals caught in break-back traps.

(a) *Treatment of live animals*

Live voles generally arrived at Oxford within a few hours of their removal from the traps in Wales. They travelled singly in tins and were

weighed and sexed on arrival. Before October 1937 some of them lost body weight or died because too little succulent food was given. After this date there were still a few deaths within the first two weeks of arrival which are likely to have been caused by these and other disturbances. Fresh and dry grass and oats were put in the traps and tins and from the spring of 1938 apple was also provided. Survival rates were much improved by this addition. Food in the laboratory consisted of hay, grain and vitaminized oil (Leslie and Ranson 1940) and at a later stage greens were added. The laboratory cages measured 10 in. x 3 in. x 3 in.

Occasionally both wild and laboratory-bred stocks died suddenly and in some numbers, often with liquid or gaseous contents of the gut. This condition is unlikely to have been caused by an infection introduced from the wild. (Our main breeding colony was housed elsewhere and never suffered these mysterious losses.)

(b) *Stages of tuberculosis*

Dr. Wells has prepared the following description of the various stages: "The grading of the tuberculous lesions of the voles examined after death has been on a purely arbitrary basis. The grades into which the disease has been divided are as follows:

Stage 1 Single small tuberculous focus (visible under x10 dissection microscope); in the great majority of cases confined to the lymph glands.

Stage 2 Multiple small tuberculous foci, mostly in the lymph glands.

Stage 3 Medium-sized multiple foci with visible spread to the vicera.

Stage 4 Extensive generalized disease.

The arbitrary nature of these stages is obvious, since it is certain, for example, that many animals classed as Stage 1 have in fact multiple small tuberculous foci when histological sections cut from various parts of the body are examined, although these foci are not visible at x10 magnification. It must also be emphasised that there is no justification for assuming that any one vole will pass through all the stages of the disease during the course of the infective process. It may well be found that a more rational classification would be into two classes—early and advanced infection—but within the limitations mentioned it has seemed desirable to retain the four stages for the present."

Since it is not easy to diagnose tuberculous animals before they have developed macroscopic lesions both these and disease-free animals are included in "stage 0." The proportion at stage 0 may be assumed to have decreased with time in captivity. The data for males and females are pooled since no differences of statistical significance can be established.

(c) *Age criterion*

No study of an epizootic can be complete without some knowledge of the age structure of the population. Unfortunately it is exceedingly difficult to determine the age of a wild mammal and the best that can be done in the present instance is to distinguish between "young" and "old." By young animals we shall mean those which have not lived through one winter. From February until May there is only the one age group, *i.e.* those born in the previous season.

Evidence from marking wild voles on Glasgwm showed that during the summer and autumn of 1937 most animals over 22.25 g. in body weight had been born the previous year. However because some old voles lost body weight and some young became pregnant this criterion is not altogether reliable, and the attempt to assess the incidence of disease according to age cannot be wholly successful. In the case of the other areas it is not known to what extent young and old can be distinguished by means of their body weights.

3. Field Evidence

(a) *Tuberculosis on Glasgwm (1936-9)*

Table I*a* shows the number of animals received from Glasgwm (according to the time at which they were caught in the live-traps), and the gross infection rate at death during the following months. Since there was a low death-rate in the laboratory it is likely that some of the infections, which were obvious several months later, would have been at stage 0 if the animals had been trapped dead. The visible infection rate in each month's catch is therefore an unsatisfactory figure which is partly a function of the time lived in captivity. An analysis of the original data shows that 79 animals died between September 1936 and 6 March 1937 and that only two were obviously infected. In the next four weeks, however, voles from the earlier samples were all killed and macroscopic lesions were found in 21 out of 46 animals.

Table I*b* shows that tuberculosis was even more frequent in the animals trapped dead in April and May and that a high incidence persisted among the adults during the summer. The young began to enter the traps in June; those taken dead showed few signs of disease, though some were carrying tubercle bacilli as proved by the development of lesions among the ones kept in the laboratory.

The adults died out during the non-breeding

TABLE I. *Distribution of macroscopic tuberculous lesions among voles on Glasgwm in 1936-8.*

		1936			1937											1938					
Date of Capture:		Sept.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	
(a) Live traps																						
Total examined		34	16	24	24	27	13	47	3	39-45*	12	6	6	5	2	.	.			.	.	Born in 1936
% infected at death		*0*	*19*	*8*	*25*	*56*	*31*	*48*		*67-58*	*61*			*46*		..	..	..	..	..	..	
Total examined		..	..	..	..	..	..	..	..	7-13*	5	15	11	37	22	7	7	34	..	26	9	Born in 1937
% infected at death		..	..	..	..	..	..	..	..	*14-8*	*20*			*30*		*71*		*68*	..	*66*		
(b) Break-back traps																						
Stage	0	..	..	..	..	..	..	20	10	21	..	8	..	1	2	2	1				..	Born in 1936
	1	..	..	..	..	..	..	14	3	2	..	2	..	2	1	..	1			..	..	
	2	..	..	..	..	..	..	14	8	5	..	5	..	1	2					..	..	
	3	..	..	..	..	..	..	7	..	6	..	..	..	..	..	..	1			..	..	
	4	..	..	..	..	..	..	10	4	..	..	1	..	1	1	...	2	..	..	..	..	
Total examined		..	..	..	..	..	..	65	25	34	..	16	..	5	6	2	5	.	.	..	..	
% infected		..	..	..	..	..	..	*69*	*60*	*38*	..	*50*	..			*67*		..	..	..	..	
Stage	0	..	..	..	..	..	..	..	..	24	..	57	..	20	15	9	8	10	10	27	13	Born in 1937
	1	..	..	..	..	..	..	..	..	..	..	2	..	3	3	3	6	3	1	14	10	
	2	..	..	..	..	..	..	..	..	..	..	..	..	2	6	3	2	6	7	21	7	
	3	..	..	..	..	..	..	..	..	..	..	..	..	1	2	..	..	8	4	11	11	
	4	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	7	3	6	3	
Total examined		..	..	..	..	..	..	..	..	24	..	59	..	26	27	15	17	34	25	79	44	
% infected		..	..	..	..	..	..	..	..	*0*	..	*3*	..	*23*	*44*	*40*	*53*	*71*	*60*	*66*	*70*	

*Two figures are given because the ages of six uninfected animals are unknown.

TABLE II. *Distribution of tuberculosis among voles of all ages in 1938-9.*
Italics show the areas in which populations decreased in 1939.

Area		1938			1939		
		May-July	Aug.-Oct.	Nov.-Jan.	Feb.-Apr.	May-July	Aug.
Marchnant*	Total examined	82	10	1	..	12	6
	No. at stages 3 & 4	19	1	..	..	..	..
	% infected, all stages	54	20	100	..	8	17
Garth-bwlch (B)	Total examined	106	75	70	106	40	3
	No. at stages 3 & 4	1	..	2	9	3	..
	% infected, all stages	9	5	10	24.5	45	0
Rhyd'r-yddan (C)	Total examined	30	22	38	35	7	..
	No. at stages 3 & 4	..	..	2	..	1	..
	% infected, all stages	0	0	5	0	14	..
Head of lake (D1 and South-east)	Total examined	39	36	47	13	2	..
	No. at stages 3 & 4	..	4†	..	2†	..	..
	% infected, all stages	3	(14)	6	(23)	0	..
Scattered areas (F)	Total examined	35	..	47	15	11	3
	No. at stages 3 & 4	4	..	4	2	5	0
	% infected, all stages	19	..	26	53	55	0
Scattered areas (E)	Total examined	17	9	17	8	12	1
	No. at stages 3 & 4	2	0	1	1	2	0
	% infected, all stages	47	0	18	75	33	0

*Including Glasgwm except in May 1938 (see Table 1).
†Some of these infections (¾ and ½ respectively) occurred in animals which died in the laboratory some months later.

season of 1937-8 (few voles live through two winters) and the infection rate increased among the young, advanced stages being common by February. During April and May 1938 about two-thirds of the population was infected. This proportion is about the same as in the previous year. If the light and heavy infections are pooled for April and May the results are almost identical for both 1937 and 1938: 42-3% at stages 1 or 2, 23-5% at stages 3 or 4.

From May 1938 onwards trap lines were set at various places outside Glasgwm, but some of them were within the same watershed, the Marchnant. Many of these voles were also infected (19 out of 32). In June and July the numbers obtained from Glasgwm were so small that the results are con-

sidered with those from the rest of the watershed: 25 out of 50 were infected. Voles were exceedingly scarce throughout the remaining months and few traps caught any voles at all (Table II).

By the method here adopted of distinguishing between the age groups, any young which exceeded 22.25 g. body weight will have been classified as old and the juvenile infection rate may have been underestimated. Nevertheless the advanced stages of disease were rare before February even if it be supposed that only young voles had been left after July. From the results of marking experiments it is known that there was a severe mortality among the young born in May and June 1937 and that most of the overwintering animals of 1937-8 had been born in July or August. The sudden rather than gradual appearance of severe lesions also suggests that a rather uniform age group was involved. In the previous summer, however, the young were probably not eliminated on the same scale. Advanced stages might therefore have been expected earlier in 1936-7 if tuberculosis had been commoner than it was during 1936.

(b) *Tuberculosis in other areas (1938-9)*

The greater part of the later trapping was with break-back traps (Table II), chiefly in the large plantations at Garth-bwlch and Rhyd'r-yddan. No marking experiments were done and it is not known whether juvenile survival rates were as poor in 1938 as they had been on Glasgwm during the corresponding peak year.

Garth-bwlch. In May 1938 only 5 out of 77 adult voles were found to be infected, about one tenth the proportion in the Marchnant watershed. Moreover all infections were in the early stages. One old animal had stage 3 lesions in June, after which there is little information until September. Three infected animals out of 53 then trapped were all heavy animals; but by November one young of the season had reached stage 3. Over the area as a whole the proportion of infected voles stayed below 25% until May 1939 and there were few advanced lesions, the first at stage 4 being found in March. In May 1939, however, half the population was infected compared with 6% in the previous year. Some of these lines covered the same ground in the two years and are considered separately in Table III, which shows that the proportion of infected animals had increased from 3 to 56% in the course of the year, though there were no advanced stages. The catches make it clear that the populations had decreased very greatly, for the same number of traps was set each year. The figures for June and August 1939 are very small, the catches having declined by about 90%.

TABLE III. *Incidence of tuberculosis in areas trapped with break-backs in May 1938 and again in May 1939.*

Stage:	0	1	2	3-4	% infected
1938 (peak year)...	57	1	1	..	3.4
1939 (decrease)....	7	1	8	..	56

Rhyd'r-yddan. Voles in this area were almost completely free from tuberculosis: from May 1938 to June 1939 three infected animals were found out of 132 received dead. Two apparently young animals had lesions at stages 3 or 4 in December. Rhyd'r-yddan populations also became scarce in 1939, only six animals being taken in a line of 53 traps which had caught 30 the previous June.

Scattered areas. The remaining trap lines were set in plantations which were too small or otherwise unsuitable for more than two or three trappings per year. Disease was infrequent in areas at the head of the lake and for 2 miles down the northeast shore. Up to December 1938 no more than one out of eight of these voles was visibly tuberculous, including 23 long-lived animals from the live traps. From January to June, 18 animals were obtained, four of them infected.

Tuberculous voles were more common elsewhere, but few conclusions can be drawn since only four out of 34 samples included more than ten voles. Two samples from area F2 suggest that the incidence approached that on Glasgwm since there were five infections among 20 voles in November and eight among 15 in March. Many voles in area F1 were also infected: three out of five in June 1938 and six out of 15 in November and December 1938. Most other lines were set in area E where again diseased animals were quite common except in September. The remaining samples came from an isolated area towards the south end of the lake (F4) and from an area 1¾ miles north-west of the head of the lake (F3). Half of these few voles were infected in June 1939.

Voles were scarce everywhere during 1939. At D1, for example, three animals were taken in 30 traps whereas 32 had been taken in a longer line of 52 traps passing through the same points in the previous June. For area E there are insufficient data to show the year of abundance.

(c) *Patchiness*

Some evidence was obtained that the disease was not distributed at random within the populations. In April and May 1937 two-thirds of the animals trapped dead were tuberculous. During the same period 50 animals were trapped alive and only 24 of them were tuberculous at death during the fol-

TABLE IV. *Distribution of tuberculosis among voles trapped in parallel lines 25 yd. apart.* (Traps set for 1-4 nights, 5 or 10 yd. apart.)

	Line:	*a*	*b*	*c*	*d*	*e*	*f*	*gh*	*i*	*j*	*k*
		Feb.	March					April			May
	Date	11	9-10	9-10	15-16	15-18	24	1-2	9	26	5
No. of animals at each stage	Stage **0**	5	10	3	7	14	6	8	4	..	3
	Stage **1**	1	..	1	..	..	..	1	..	..	1
	Stage **2**	3	3	1	..	1	..	..	..	..	1
	Stage **3**	1	2	4	..	1	..	..	..	1	1
	Stage **4**	..	1	5	2	..	..	1	..	..	1
	Total incidence	5/10	6/16	11/14	2/9	2/16	0/6	2/10*	0/4	1/1	4/7
	Total incidence (%)	42		live traps				20			
		West		←Total distance 250 yd.→						East	

*Pooled result from two lines.

lowing weeks. The proportion infected is significantly lower in the live trapped animals, whereas, if tuberculosis had been randomly distributed throughout Glasgwm, macroscopic lesions would have become relatively more frequent in the samples kept in captivity.

A second example is shown in Table IV. In February 1939 five infected animals were found out of 10 captured in line *a*, the first of a series of parallel lines at Garth-bwlch. In line *b*, 25 yd. to the east, there were six infections among 16 voles captured early in the next month. Two lines of live traps (*c*, *d*) were set still further east. These voles lived for a long time in the laboratory (Table V) so that the high proportion of infected animals in line *c* is not comparable with the results from the break-backs. However, the voles from line *d* also lived about as long and only two out of nine were infected at death.

This drop in infection rate within 25 yd. was confirmed by the results of further parallel lines of break-backs (*e-j*) during March and April, the total number of infections being only five out of 37, despite the greater length of time during which lesions could have been developing. A final line in May gave a rather higher rate (four out of seven). Such differences in the distribution of disease must be expected in a species whose members spend most of their lives within a restricted area. (The range of voles marked on Glasgwm seldom exceeded 10-15 yd. diameter, though it is slightly greater in some populations).

(d) *Summary*

Tuberculosis was unevenly distributed in time and space. During the non-breeding season (September or October to March) the proportion of infected voles rose to a maximum which, from the spring onwards, was maintained in the animals which had overwintered. In the population as a whole, however, the incidence of tuberculosis fell during the summer because of the continual entry of young, in whom advanced lesions were rare until several months after breeding had ended.

Tuberculosis became more frequent on Glasgwm after 1936 and on Garth-bwlch after 1938.

Disease was almost completely absent from some areas and very prevalent in others; its frequency also varied, though to a smaller extent, between samples from within areas.

4. LABORATORY EVIDENCE

(a) *Survival*

The present data are not suitable for showing how the disease affected survival in the laboratory. The average length of life cannot be taken because animals were received at all ages and seasons and therefore with different probabilities of survival. The occasional simultaneous deaths from other causes (Section 2a) affected animals after different periods in the laboratory and others were killed for examination. In March 1939, however, voles were captured at about the same time in the two adjacent lines already discussed (Table IV), and we may compare survival rates between the tuberculous and relatively healthy groups. Table V shows that there was little difference in survival rate before August, by which time the animals would have been almost one year old. The final survivors, however, were all free from disease. No such comparisons can be made from the data for 1936-8, but as observed above many of the longest-lived animals were tuberculous. The survival rate of the animals in the laboratory was very much better than that of the field populations and tuberculosis therefore had a greater chance of developing to a lethal stage. Even so, the effect of tuberculosis upon the death-rate was small in comparison with that of the other causes of death in

TABLE V. *Survival of tuberculous and healthy voles in captivity (trapped 9-16 March 1939).*

Group	Original No. of animals	No. of survivors at the end of each month										
		March	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
Mostly tuberculous	14	12	10	10	8	8	3	2	2	2	1	0*
Relatively healthy	9	8	6	5	5	5	3	1	0	..	..	..
	Total infected	Stage of tuberculosis at death										
Mostly tuberculous	11	0, 1	3, 4	..	3, 4	..	2, 3, 3, 4, 4,	4	..	..	0	0
Relatively healthy	2	0	0, 4	0	..	..	0, 0	0, 4	0	..	..	..

*Killed 20 January 1940.

captivity. (The causes of death among uninfected voles could not be determined.)

Some further information is provided by the time elapsing between capture and death at various stages of infection. It may be assumed that the length of time between infection and the development of a certain stage of tuberculosis is distributed about some mean value; but neither the mean nor its distribution can be determined since we do not know when the animals became infected or how soon afterwards they were trapped. No information can therefore be obtained about the more rapid rates at which tuberculosis may develop. However, by examining the tail-end of the distribution of intervals between capture and death we may learn something about the slower rates of the infective process. Table VI shows the six longest times of survival of voles which died with lesions at stages 1, 2, 3 or 4.

TABLE VI. *The six maximum intervals between capture and death at each stage of tuberculosis.*

Stage	Weeks lived in captivity					
1.....	7	10	11	13	15	16
2.....	17	18	18	18	23	37
3.....	17	21	22	23	31	31
4.....	27	28	31	39	41	53

(Since these figures are the tail-end of some unknown frequency distribution it is obvious that no mean value can be taken.) It is seen that one animal had been infected for at least 16 weeks and still had no more than a single macroscopic focus and that another animal had developed nothing worse than stage 2 lesions after 37 weeks. However, most of these animals had stage 3 lesions after about 20 weeks and the final stage was more common after 30 weeks. These data tend to underestimate the length of the infective process in these individuals as it is unlikely that they had all been trapped immediately after becoming infected.

These cases have been selected to show the slower rates of development in the laboratory, but from the field evidence we have also seen that faster rates were rare. In fact the interval between birth in July or August and the common appearance of advanced lesions in February is also between 20 and 30 weeks.

5. Discussion

(a) *Tuberculosis*

The absence of any great effect of the disease upon survival in the laboratory does not necessarily mean that infected animals were not handicapped in the wild. On the contrary it will be noted that the proportion of animals at stages 3 and 4 does not increase after February (Table I). If the disease were entirely without effect an increasing proportion of animals would be expected in these groups. Some additional mortality through tuberculosis may certainly be postulated, but its effect is not necessarily very great (Wells 1946); for the probability of dying from the disease seems to be low in comparison with that from other hazards.

It is nevertheless instructive to set up the hypothesis that the abnormal mortality of 1938 was caused by an epizootic of tuberculosis. Given only the data for Glasgwm in the spring of 1938 this view is not unreasonable. For example Leslie and Ranson (1940) have suggested that the time between March and May or June is particularly crucial and that a population would be seriously reduced through further increases in the death-rate. However, since the present data are not confined to one year or one population it is easy to refute the hypothesis that tuberculosis caused the decrease. Thus on Glasgwm, tuberculosis was no more prevalent during the decrease in 1938 than it had been in 1937 when numbers remained high (Table I); furthermore the disease was almost absent from some areas where a similar decrease occurred in 1939 (Table II).

Although tuberculosis alone does not explain why the voles declined on Glasgwm in 1938 it is

not necessarily true that the effect of the disease was the same as it had been in the previous year. As shown elsewhere (Chitty 1952) the Glasgwm voles seem to have been in poor physiological condition in 1938 and may well have been less resistant to tuberculosis. Because of the totally different survival rates in the two years and because of the sampling errors already discussed no conclusions of this nature can be drawn from the present set of data. Nevertheless, while it is true that the proportion infected in the samples was rather similar in both years we cannot exclude the possibility that, compared with uninfected animals, those with advanced tuberculosis were at a greater disadvantage in 1938 than in 1937.

It cannot be stated that no other infectious disease was responsible for the mortalities of 1938 and 1939. It is clear, however, that the mere presence of some pathological condition at a time of population decrease cannot be admitted as proof that one has caused the other. This distinction between contributory and necessary causes of mortality has not always been recognized; and at this point it will be advisable to classify the types of observations that may be made in studying an epizootic. Four types may be recognized as shown in the following table:

	Disease widespread	Disease largely or entirely absent
Severe mortality	Type 1	Type 2
No severe mortality	Type 3	Type 4

The observations on vole tuberculosis were of types 1, 2 and 3 and so the hypothesis was rejected that this disease was a necessary mortality factor. Evidence of type 4 was also obtained, followed next year by type 1. For example, Table III shows that a decline in numbers was associated with an increase of 16 times in the rate of infection. In this instance, of course, there is additional information to show that tuberculosis could not have caused the mortality; but diseases about which much less may be known probably spread in a similar way among crowded populations and may well give rise to the belief that disease is responsible for a decline in numbers. It would clearly be rash to draw any such conclusions unless there were further evidence to prove that the populations would not have declined had there been no spread of disease. (The required evidence may be less difficult to obtain in the case of a species whose numbers seldom fluctuate violently.)

(b) *Problems of inference in the study of epizootics*

Elton (1942) has shown that infectious disease is unlikely to be the cause of the regular recurrence of population decrease in voles. He has also shown that there is some doubt about the part played by a protozoan parasite, *Toxoplasma,* "which is reported in three different cycle crashes and is not seen again" (p. 201). At Mr. Elton's request I have therefore re-examined the evidence that *Toxoplasma* caused mortality among certain populations of field voles. I have also reviewed the claim, accepted for many years, that numbers of the red grouse are periodically reduced by outbreaks of strongylosis. The purpose of using these examples is to question the validity of inferring, from limited types of observation, that infectious disease controls population density.

Findlay and Middleton (1934) obtained samples of *Microtus* from two areas. In one of these areas (Argyll), voles had recently declined from great abundance, but at the other (Lake Vyrnwy), "the mortality which started in March did not continue, and, although the voles were greatly reduced at that time, they increased again throughout the summer of 1933. In October 1933 the vole population at Lake Vyrnwy appeared to be nearly equal to that of the corresponding period in 1932 . . ." The decrease at Lake Vyrnwy was not, in fact, of the same kind as in Argyll, and from our vantage point in time we see that it may have been no greater than is to be expected in a non-breeding season (Chitty 1952, Fig. 4). Since the proportion infected with *Toxoplasma* was actually lower in samples from Argyll than from Lake Vyrnwy we may conclude that a condition associated with decrease in one area was without effect in the other. We must therefore examine the reasons for believing that an epizootic was in progress at either place.

Voles were sent from the field to London and Table VII gives the survivorship of the 60 animals received. It is seen that 95% of the animals had died within two weeks: a high rate which was independent of the post-mortem findings. That this death-rate was abnormal may be gathered from Table V, from Leslie and Ranson (1940), from Chitty (1952) and from the field evidence for Lake Vyrnwy in 1933.

An insight into the possible causes of this laboratory mortality is provided by Elton, Davis, and Findlay (1935) in a later study. About 40% of the animals captured were found dead in the traps and the survivors were then placed in groups of up to 15 animals for at least part of the time before arrival in London. There were few deaths among the grouped voles trapped in January and February, but 41% died before arrival in May. "We are probably right, therefore, in concluding that the mortality between the traps and despatch to London mainly reflected the progress of the main epidemic" (p. 286). It seems at least equally

TABLE VII. *Number of voles alive at the end of each week (from Findlay & Middleton, 1934).*

	Day:	0	7	14	21	23
Lake Vyrnwy	+	9	4	1	1	0
	−	3	1	0	..	..
	d.	7	2	1	0	..
Argyll	+	12	5	0	..	..
	−	12	4	0	..	..
	d.	17	5	1	0	..
Total alive		60	21	3	1	0

+ = *Toxoplasma* found on post-mortem.
− = No *Toxoplasma* found.
d. = Died overnight; too decomposed for examination.

likely, however, that a boxful of strange voles of mixed sexes might get along together less well in the breeding season than in January or February, and that many of the deaths were due to fighting (Clarke 1953*a*). Whatever the reasons, only 126 survivors reached London out of a total of 270 voles which had entered the traps. It seems possible that the factors responsible for an unnatural mortality as great as this might also have affected the survival rate of the remaining animals. The proportion dying within two weeks of arrival rose from 10% in January to 69% in April. Fourteen voles were infected out of 25 suitable for examination.

There are also certain doubts about the natural occurrence of any toxoplasms as all (Elton 1942, p. 196), and the pathological evidence itself also needs to be re-examined. For example the nervous symptoms described are not unlike those seen in voles dying from cold, hunger or thirst; and according to Frenkel and Friedlander (1951, p. 65) the organism was not *Toxoplasma*.

To sum up: (1) voles were dying at an abnormal rate in the laboratory, most likely because they had suffered during trapping and transport (2) they died equally fast whether or not they were infected (3) the proportion infected was no higher in samples from Scottish areas where there was a heavy natural mortality than from Lake Vyrnwy where there was not (4) there is no formal proof that *Toxoplasma* occurred in these voles either in the field or after capture.

We may now consider another instance in which population decrease has been explained by the presence of pathogenic organisms. Periodic reductions in the numbers of red grouse (*Lagopus scoticus*) have been attributed to the effect of the nematode, *Trichostrongylosus pergracilis* (Cobbold), upon the adults and to coccidiosis (*Eimeria* sp.) upon the young (Committee of Inquiry . . . , 1911). Nearly all adult grouse were infected with strongyles, and during outbreaks of disease the birds found dead were all emaciated. In complete contrast to these findings, previous investigators had remarked how often birds died in apparently good health at times of heavy mortality (Farquharson 1874*b*; Wilson 1875; Macdonald 1883; Klein 1892). These observations seem too definite to have been disputed, however wrongly they had been interpreted by Professor Klein (Wilson and Leslie 1911, pp. 199-206). Mackenzie (1952) has also shown that strongylosis is not always associated with periodic decrease of grouse.

It appears therefore that two entirely different groups of mortality factors may cause the periodic decimation of the red grouse. In some cases parasites are obviously responsible for the emaciated condition at death, in other cases the birds die from unknown causes. Moreover from a survey of the literature on other species of game birds it appears that mortality factors vary so much according to local conditions that no conclusions can be reached that apply to populations in general. In the next section the problem is therefore restated in more general terms.

(c) *Predisposing causes of death*

As has already been pointed out in Section 5(a), type 1 evidence that disease (or indeed any other specific mortality factor) is associated with population decrease is no proof that the populations would not in any event have suffered heavy losses. The Committee of Inquiry was not therefore justified in concluding that strongylosis and coccidiosis were necessarily responsible for the decline of the grouse, although they were not lucky enough to encounter evidence of type 2 by which to reject the idea. They realized, however, that infected populations did not always decrease (type 3 evidence) and that the spread of parasites alone did not account for a change in mortality rate. The important suggestion was therefore made that there must also have been changes in the powers of resistance of the host (Lovat 1911, pp. 374-6) and attempts were made to see if outbreaks of disease were brought about by unfavorable conditions, particularly in weather and food. Some success was naturally achieved since the British weather is likely to be abnormal at some critical time in an animal's life; but the evidence was far from convincing (Leslie and Berry 1911, pp. 118-20).

The idea that there might be changes from year to year in the powers of resistance of red grouse populations had already been expressed by Young (1868) and by Cobbold (in Farquharson, 1874*a*). Young's views are of particular interest: "The mortality [in the red grouse] is, in fact, due to mal-nutrition, to a cachetic state transmitted from

parent to offspring, and predisposing the young to suffer from influences such as severity of seasons or temporary scarcity of food, which under other circumstances they would have resisted successfully." Siivonen (1952) has now provided evidence for various species of tetraonids in Finland which leads him to a similar view. He observes that at times of severe mortality the clutch size is low, the eggs hatch less well and fewer of the young survive. He concludes that there is "a general weakness of the progeny" and that this is "inevitable even before laying." One other author (King 1937) has also reached the same conclusion about ruffed grouse, but he admitted that he was unable to prove his point. King stated: "probably the greatest loss of young birds is due to a condition existing before they are hatched."

Other authors have clearly been puzzled by their inability to find abnormal environmental circumstances to account for mortality among game birds, especially chicks. Leslie and Berry (1911) refer to "the puzzling fact that it is only where the parent birds are unhealthy that the young stock seems to be seriously reduced by bad weather in the breeding season." Middleton (1936) observed that strongylosis among partridges "appears to prevent them rearing their broods even if they hatch them." Clarke (1936) reports for the ruffed grouse: "even though the first year of dying-off in an area has reduced numbers to a point where the birds may be regarded as scarce, the succeeding year may show a similar reduction of summer flocks." In the case of the bobwhite quail Errington (1945) notes that in the winter of 1936-7 a low population "did not appear to be well accommodated under nonemergency conditions."

Further problems and ideas are discussed by Bump, Darrow, Edminster, and Crissey (1947) in their study of the ruffed grouse. Darrow (p. 575) suggests that "lowered vitality among the young" is characteristic of periods of heavy mortality. In certain years there was also an unusually high death-rate among chicks which had been hatched in captivity (Bump, pp. 482, 878); but the causes of death could not be determined. Crissey (pp. 305-6) points out that unfavorable temperatures have preceded periods of scarcity among ruffed grouse in New York State, but that similar conditions have occurred without corresponding changes in numbers. Darrow (p. 577) suggests, if I interpret him correctly, that when populations have reached high levels of abundance they become unusually vulnerable to a number of mortality factors, especially those associated with bad weather.

Christian (1950) discusses the possible changes in the endocrine system which may be produced as the result of stress among crowded populations of mammals. It is clear, however, that we also have to solve the problem of an abnormally high death-rate among mammals and birds which are living under environmental conditions which are not abnormally severe. The suggestion which emerges from my own work on the vole and from the few extracts already quoted from the literature on game birds is as follows: that the probability of survival of the young of certain animals is largely predetermined by the physiological condition of their parents. As Clarke (1953*b*) has pointed out we have no hypothesis to suggest how the offspring derive their abnormal condition, though Calhoun (1949) has evidence that such effects may be produced experimentally in the brown rat.

About the nature of the physiological disturbances we have at present little evidence. Green, Larson, and Bell (1939) believed that a profound disturbance of the carbohydrate metabolism was to be found in declining populations of snowshoe hares: "They appeared to be abnormal, suffering from a condition that caused them to succumb when subjected to stress." In the case of the game birds it seems possible that they too may be suffering from deranged metabolic processes.

We should now perhaps regard infectious disease as only one of a complex group of biotic and physical factors any one of which may be the actual cause of death in physiologically deranged animals. The individual contribution of these numerous factors to the death-rate may therefore be entirely dependent upon the accidents of local conditions. The problem then becomes of more general interest, *i.e.* to determine what change in the population makes its members more vulnerable to normal hazards.

In order to find out if there is any truth in this hypothesis we need information on the following matters: (1) the changes brought about in behavior and population structure by an increase in numbers; (2) the physiological disturbances—such as those discussed by Christian (1950)—which seem to occur at certain stages of population growth; (3) the physiological disturbances which seem to be transmitted from one generation to another—for there is no reason to suppose that (2) and (3) are the same; (4) the particular mortality factors such as cold, hunger and disease to which the animals become less resistant. In addition to the field observations a number of experimental procedures are called for; the first of such studies has been carried out by Clarke (1953*a*).

6. Acknowledgments

I wish it to be clear that I have made none of the post-mortem examinations but have merely analyzed records placed at my disposal. I am grate-

ful to Dr. Wells for this and for much other help and we both thank Mr. Charles Elton, F.R.S., for starting us on this enquiry. Comments on the manuscript by Mr. P. H. Leslie have also been most valuable. Elsewhere Dr. Wells and I have fully acknowledged the help we received from the Agricultural and Medical Research Councils and from Liverpool Corporation at Lake Vyrnwy.

7. Summary

1. Tables I and II give details about 952 field voles (*Microtus agrestis*) which were examined by Dr. A. Q. Wells for evidence of an infectious disease which might account for the violent changes in numbers to which this species is subject. These pathological data have been analysed in relation to the mortalities observed at Lake Vyrnwy, Montgomeryshire.

2. In one area tuberculosis was rare during 1936 but became obvious in about two-thirds of the spring population of 1937. Animals born in the early part of 1937 mostly died from other causes so that only the later young lived long enough to become heavily infected. Advanced tuberculosis took at least six months to become common (this slow progress is consistent with laboratory observations) but was again prevalent in the spring of 1938. On this occasion the spread of the epizootic coincided with a decline in population density.

3. Other vole populations remained abundant throughout 1938 but declined in 1939. Advanced tuberculosis was comparatively rare, though in one area the frequency of the early stages had increased from 3 to 56% under conditions of high numbers.

4. The frequency of tuberculosis also varied within populations, as is to be expected from the vole's relatively confined movements.

5. The survival rate of wild voles kept in the laboratory was not greatly reduced by heavy infections of tubercle bacilli, and under field conditions other mortality factors seem to have been of greater significance.

6. Resistance to tuberculosis may have varied in the field with certain changes in physiological condition, but tuberculosis itself did not account for the abnormal mortalities of 1938 and 1939.

7. The difficulties of drawing valid inferences from field data are illustrated by examples from the present study and from previous work on diseases in the vole and the red grouse. The occurrence of an epizootic at a time of severe mortality is shown to be insufficient evidence that infectious disease controls the density of natural populations.

8. Infectious disease, it is suggested, is only one of several mortality factors to which certain mammals and game birds are less resistant at some population densities than at others. The chances of survival are probably influenced by the physiological condition of the parents.

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PLOTLESS SAMPLING TRIALS IN APPALACHIAN FOREST TYPES[1]

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Quantitative data are essential to an adequate characterization of vegetation for most purposes, and only through the use of quantitative data can the problem of classifying vegetation stands into categories ("associations," *sensu latiore*) be approached objectively. For these reasons, much attention has been devoted to vegetation sampling techniques, and any method which promises an increase in efficiency is welcomed hopefully. An effective method for general use in ecological survey work should be (1) adaptable for use in rapid reconnaissance as well as in intensive study of small areas, (2) operable by one person at a reasonably efficient level, and (3) susceptible to statistical measures of variability, so that confidence limits can be established for stand and composition estimates, and appropriate sampling intensity be determined.

A promising plotless forest sampling technique developed in Germany (Bitterlich 1948) was recently presented to the American forestry profession (Grosenbaugh 1952a, 1952b). Its features commended it as an ecological research technique. Therefore, it was felt worthwhile to test its usefulness in Appalachian forest types by comparing it with conventional plot sampling and with plotless sampling by random pairs as described by Cottam and Curtis (1949). Trials were made in both high altitude spruce-fir and mid-altitude deciduous forest in the Great Smoky Mountains in eastern Tennessee, and supplementary data are presented from an oak-hickory stand in the Appalachian Valley near Norris, Tennessee, and from a mountain cloud forest stand in southern Tamaulipas, Mexico.

[1] Contribution from the Botanical Laboratory, The University of Tennessee, N. Ser. 150.

SPRUCE-FIR, 1952

The Mt. Mingus spruce-fir stand, Great Smoky Mountains National Park, previously studied by Cain (1935) and by Oosting and Billings (1951), was selected because it represented a relatively well-known, simple, and uniform forest type. It had been specifically suggested by Cottam and Curtis (1949) that the random pairs method should be tested in denser vegetation stands than those they had studied in Wisconsin, such as "the southern Appalachian spruce-fir." The sampling area consisted of a linear series of 40 x 40 meter blocks which extended approximately one-half mile northwest from Indian Gap, between the 5200 and 5300 foot contours on the southwesterly slope of Mt. Mingus, and probably lay between the two strips of samples used by the previous investigators. Two sampling points were located at random within each block. The two kinds of plotless samples were taken from these points as described in the following paragraphs, and circular plots one-fortieth acre in area (approximately 100 sq. m.) were centered on them. Tenth-acre plots were centered on 24 of these points, at the southeastern end of the series.

The variable-radius plotless method described by Grosenbaugh is based on the principle of point sampling. Since point sampling is not efficient due to the very small fraction of the area actually occupied by tree trunks, a simple device is used to increase the effective size of each point sample without altering the proportional relationship. A

hand-held angle-gauge is used to determine what trees are within a distance no greater than 33 times their diameter from the sampling point, and all trees which subtend an angle greater than that of the angle-gauge are tallied. The probability that any tree will be included in the count is still proportional to its basal area, and the angle is so selected that the tally need only be multiplied by a factor of 10 to yield basal area in square feet per acre. Thus, a tally of 18 trees would indicate 180 sq. ft. basal area per acre; 14 would indicate 140 sq. ft. per acre; 8 spruce trees tallied would indicate 80 sq. ft. of spruce per acre. Slope corrections based on the secant of the slope angle are recommended by Grosenbaugh and have been used in the trials here reported.

The random pairs method makes use of two-tree samples selected as follows: the first is the tree nearest the sample point; the second is the tree nearest to the first outside the 160° sector bisected by a line from the sample point to the first tree. Diameters of the sample trees and distances between them provide the basis for computing stand composition. The standard practice in Wisconsin where the method was developed and where it has been used extensively has been to use only trees 4 inches or more in diameter, to use 40 points providing 80 trees per stand, and presumably to base stand estimates on average basal area of sample trees and average spacing, the method used in obtaining the values in the last column of item 3, Table I.

Table I presents a comparison of results from the different sets of samples. Scientific names follow the usage of Fernald (1950). Disappointingly poor agreement among the results of different methods is shown in the stand data of item 3, Table I. Some death and windthrow of post-mature spruce have occurred since Cain's study was made, but it is not so easy to rationalize differences in results of sampling at the same points and at the same time.

Since it was desired to compare confidence intervals as well as estimates of central tendency among the different sampling methods (Table II), the random pairs were also treated as individual samples in the present study. It was found that the mean of these values was quite high (422.6 sq. ft. basal area per acre) and the distribution so badly skewed (median 206.5 sq. ft. per acre) that computation of standard error was not pertinent. This led to the further study of random pairs and

TABLE I. *Spruce-fir stand data, Mt. Mingus, Great Smoky Mountains*

	Cain 1935	Oosting and Billings 1951†	1952 Comparison			
			1/10 A. plots	1/40 A. plots	Variable-radius plotless	Random pairs
(1) Total sample area (acres)	2.5	.25	2.4	1.0	....	....
(2) Total trees 4″ or over	...	57	629	363	727*	80
(3) Basal area, sq. ft. per acre						
Total	329.2	242.6	218.5	293.7	203.5	203.5
Standard error	±11.5	±25.7	±15.1	±25.6	±7.5	....
Red spruce (*Picea rubens*)	292.7	179.8	176.4	236.0	153.2	182.7
Fraser fir (*Abies fraseri*)	24.1	50.5	35.9	44.1	41.6	20.0
Yellow birch (*Betula lutea*)	8.1	8.1	4.0	9.4	5.9	0.8
Others	3.8	4.2	2.2	4.3	2.0	0.0
(4) Density, trees/acre, 4″ or over	....	228	262	363	....	213
(5) Basal area (sq. ft.) of average tree 4″ or over	....	.97	.79	.81	....	.96
(6) Percentage composition (basal area)						
Red spruce (*Picea rubens*)	88.9	74.0	80.7	80.3	75.3	89.7
Fraser fir (*Abies fraseri*)	7.4	20.9	16.4	15.0	20.5	9.8
Others	3.7	5.1	2.9	4.7	4.2	0.4
(7) Species frequency, percentage						
Red spruce (*Picea rubens*)	100	100	100	100	100	85
Fraser fir (*Abies fraseri*)	100	100	100	100	95	68
Yellow birch (*Betula lutea*)	80	40	67	78	40	5
Serviceberry (*Amelanchier laevis*)	60	10	50	63	13	0
Mountain holly (*Ilex montana*)	60	60	38	58	2	0
Mountain ash (*Pyrus americana*)	30	10	25	50	2	0
Mountain maple (*Acer spicatum*)	0	30	0	0	0	0
Striped maple (*Acer pensylvanicum*)	0	0	17	0	0	0
Beech (*Fagus grandifolia*)	0	0	8	0	0	0

†Data for Oosting and Billings' samples were computed in part from their unpublished field data which were kindly lent to the writer.
*Including a few smaller trees.

TABLE II. *Stand estimates in sq. ft. basal area per acre, based on different methods of sampling and computation, spruce-fir type, Great Smoky Mountains, 1952*

	Lower 95% confidence limit	Central tendency	Upper 95% confidence limit
Plots, tenth-acre (24)			
mean	187.3	218.5	249.7
median	163.0	227.4	263.7
Plotless, variable-radius (40)			
mean	188.4	203.5	218.6
median	183.0	205.4	229.0
Random pairs (40)			
mean, untransformed data	.....	422.6	.....
mean, transformed data	175.0	240.4	330.4
median	139.1	206.5	391.0
Plots, fortieth-acre (40)			
mean, untransformed data	(242.1)*	293.7	(345.4)*
mean, transformed data	203.3	247.8	302.0
median	189.6	243.2	374.0

*Not valid estimates, but the results obtained if standard computational procedures, assuming normal distribution, are used.

other small samples previously reported (Shanks 1953) and the logarithmic transformation of skewed distributions into approximately normal distributions as illustrated later (Figures 2 and 3) The relatively high stand values in Table I from fortieth-acre plots, computed in conventional manner, also attracted attention. It was found that the fortieth-acre plots were also characterized by a skewed distribution of stand values, and that the mean of their transformed values came into close agreement with the median (Table II). It seems that the random pair bias is simply the extreme case of a general small-sample bias which may be satisfactorily eliminated by logarithmic transformation, an inference consistent with the evidence brought together from a number of sources in the review papers of Ashby (1936) and Goodall (1952). It may be noted from Table II that the medains of the various sample series are clustered in a much narrower range than the means, and that the greatest differences between medians and means exist in the smaller samples. Differences in effective sample size are indicated by the fact that the variable-radius plotless samples averaged about 18 trees per sample and the 1/40 A. plots about 9 trees per sample as compared with the 2-tree sample of a "random pair." The variable-radius plotless samples, in contrast with the smaller samples, approximated a normal distribution, and conventional statistical procedures could be appropriately applied, as suggested by Grosenbaugh. In this example, it is estimated that only 7 samples would be needed to give a standard error of ±10% of the mean, and about 25 samples to give ±5%.

Item 6 of Table I shows general agreement among the comparative estimates of dominance based on the different sets of samples, but together with item 3 suggests that the two-tree samples may result in a differential bias in favor of the larger-sized spruce (see also data on *buckeye* in Table V).

The use of "order statistics" offers a promising evasion of the labor transformation of skewed distributions, for normal distribution is not required for the use of the median and its confidence intervals (Dixon and Massey 1951). Where the data are used for general descriptive purposes, a high degree of precision is usually not as important as comparability, and the less precise but easier order statistics may be preferable whether the data are normally distributed or not. Table III, abridged from Dixon and Massey (1951), gives 95% confidence limits for the median for common numbers of samples.

TABLE III. *Confidence limits for the median, abridged from Dixon and Massey (1951)*

Number of samples	Ranks of values exceeded by less than 5% of the medians
25	8, 18
40	14, 27
50	18, 33
60	22, 39

SUPPLEMENTARY DATA, 1952

A further check on variable-radius plotless sampling was obtained from data assembled by Donald L. Hilbert in 1952, to characterize an area along Clear Creek near Norris, Tennessee, where a small mammal population study was to be made. A nine-acre area of oak-hickory forest was subdivided by a grid into 1/16 acre plots. Four rows running up and down hill, totalling 48 plots, were used, and 42 systematically distributed points were used as points of origin for variable-radius plotless samples. The stand estimate by plot sampling was 110 ±7.8 sq. ft. basal area per acre, by plotless sampling 118 ±3.8 sq. ft. The plot sampling required 18 man-hours in addition to the time required to lay out the plots, plotless sampling 6 man-hours. The estimates of stand per acre agree reasonably well, but the relatively higher yield of information from plotless sampling is again reflected in its narrower confidence limits for a similar number of samples. It would have taken about 60 plots to reduce the standard error of the plot sampling to the 5% level already attained in the plotless sampling, raising the time required by another 25%.

It is evident that variable-radius plotless sampling is an efficient means of assembling forest stand data, in terms of square feet basal area per acre and percentage composition and their variability. However, these are not the only desiderata in ecological community analysis. Can the method yield additional descriptive data on stand structure and species frequency?

Frequency data are directly available, but they differ from the usual frequency data in that they are not based on a single specified plot size but on the 1/33 ratio of tree diameter to effective plot radius. Thus, they express the frequency of effective vegetational contribution rather than frequency of botanical presence. Species frequencies in the Mt. Mingus spruce-fir by the various methods are compared in item 7 of Table I. Although the figures differ, species ranks are similar and similar inferences concerning stand organization are supported.

Information on number of trees per acre and distribution by size classes may be obtained from plotless sampling by the simple procedure of estimating diameter and tallying each tree in its appropriate diameter class. Basal area per acre in each diameter class is then directly available, and number of trees per acre in each class may be readily computed for the total stand, for individual species, or for groups of species. Six-inch diameter classes have proved quite adequate for this purpose.

Thus plotless sampling may provide data for the construction of conventional phytographs which display on their four radii comparative density, frequency, basal area and size classes. The data presented in Table IV and and Figures 1 and 2, based on a cloud forest stand in the Sierra de Guatemala above Gómez Farías, Tamaulipas, Mexico. were derived entirely from plotless samples. In this case, neither time nor personnel for plot sampling was available, yet an adequate descriptive picture with quantitative support was provided. This is from the area known as the "Parque," near Ojo de Agua de los Indios, in the general area described by Hernández, Crum, Fox, and Sharp (1951).

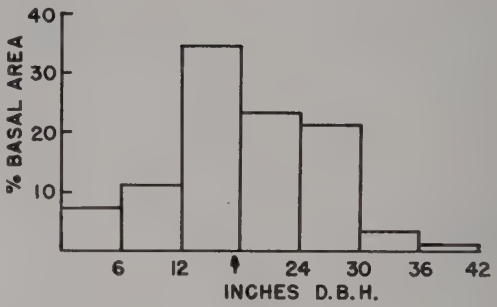

FIG. 2. Distribution of basal area by diameter classes, cloud forest stand, Sierra de Guatemala.

TABLE IV. *Data from plotless sampling, cloud forest stand, Sierra de Guatemala*

	Beech (*Fagus mexicana* Martinez)	Sweet Gum (*Liquidambar styraciflua* L.)	Red Oak (*Quercus* sp.)	Magnolia (*Magnolia schiedeana* Schlecht.)	
Data for phytographs					
% Density (over 6")	30.5	18.6	22.4	9.4	
% Frequency	100.0	100.0	94.0	50.0	
% Size classes	100.0	80.0	100.0	80.0	
% Basal area	29.6	24.5	22.0	5.7	
Stand data					Totals
Mean no. trees/acre over 6"	20.5	12.5	15.0	6.3	67
Mean basal area, sq. ft./A.	30.1	25.0	22.4	5.8	102.0
Standard error	±4.6	±3.5	±3.9	...	±5.2

COVE HARDWOOD FOREST, 1953

A mid-altitude deciduous forest type in the Great Smoky Mountains, dominated by yellow buckeye (*Aesculus octandra*), basswood (*Tilia heterophylla*) and sugar maple (*Acer saccharum*), was selected for the 1953 trials. Three series of samples were taken between the 3200 and 3500 foot contours in the upper Sugarlands Valley along the Park Headquarters—Newfound Gap highway,

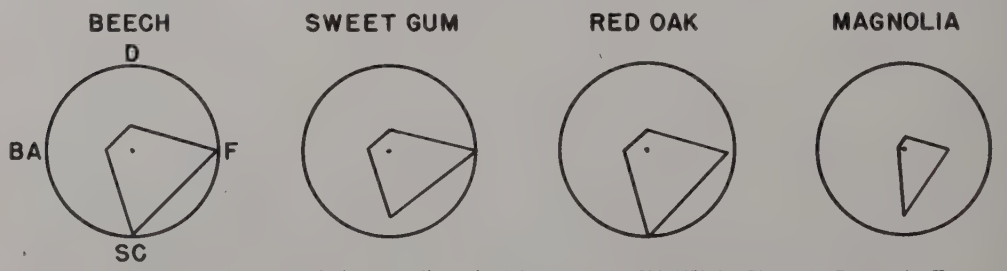

FIG. 1. Phytographs based on plotless sampling, cloud forest stand, 4290-4450 ft., Sierra de Guatemala, Tamaulipas, Mexico, 1952.

from the coves and rocky lower slope above and below the lower tunnel. These sites had a southerly exposure, but were somewhat sheltered by the high ridge of Sugarland Mountain across the valley from them. The buckeye-basswood-sugar maple forest type is a well-marked association-segregate of the mixed mesophytic forest (Braun 1950), a variant of the buckeye-basswood segregate recognized by Cain (1943) in his analyses of the cove hardwood forest complex of the Greenbrier region a few miles eastward. The plotless samples in the following analysis are combined from the three stands, the tenth-acre plot samples from two of the three.

Species composition

While variable-radius and plot sampling agree quite closely (Table V), the relative density data for buckeye and basswood are reversed in the data from random pairs. Examination of the data shows that this could not be due to the lower size limit, and another explanation must be sought.

TABLE V. *Relative densities of important species (% of total stems), and relative basal area (% of total) by different sampling methods; cove hardwood forest, 1953*

	Tenth-acre plots (217 trees over 6″)	Variable-radius plotless (573 trees over 6″)	Random pairs (80 trees over 4″)
(A) Relative density			
Aesculus octandra	23.5	22.2	32.0
Tilia heterophylla	37.4	34.6	26.0
Acer saccharum	16.6	17.8	22.0
Halesia carolina	6.4	7.5	6.0
Quercus rubra	2.3	4.2	2.0
Carya glabra	2.3	3.8	2.0
Others	11.5	9.9	10.0
(B) Relative basal area			
Aesculus octandra	37.3	31.5	48.8
Tilia heterophylla	27.9	27.5	11.8
Acer saccharum	14.6	16.5	22.3
Halesia carolina	3.4	3.9	4.7
Quercus rubra	5.0	7.9	6.5
Carya glabra	1.4	3.0	3.6
Others	10.4	9.7	2.3

The random pair samples consisted of unit trees rather than unit areas and, if all species were similarly dispersed, should constitute a proportionate sample of species composition. However, in this case basswood differs markedly from the other species in distribution, being typically clumped because of sprout regeneration. If a basswood clump is encountered in random pair sampling, the "excluding angle" (Cottam and Curtis 1949) is likely in most cases to exclude all but one tree of the clump, resulting in the underrepresentation of basswood illustrated in Table V, with relative overrepresentation of associated species. This relationship is even more striking with respect to basal area than to density, and is consistent with Table I, item 6, which also shows differential bias in favor of the species with best representation in larger size classes, in that case spruce.

It may be noted that the order of abundance of buckeye and basswood in Table V (A) is reversed from the usual order in the type name, which is based on dominance as expressed in crown cover or basal area. Table V (B) illustrates the shift of buckeye to first rank due to the relatively large size of many of the buckeye trees when basal area is used instead of density. This forest type appears to have more trees of basswood, but more basal area or volume of buckeye, a structural characteristic not revealed by random pair sampling.

Stand data

Individual plotless samples varied greatly in tree spacing and thus in area represented. Distances between trees among the random pairs did not deviate greatly from the normal distribution assumed by Cottam and Curtis (1949), as they apparently did in the historical data on oak openings studied by Cottam (1949). However, the derived figures for trees per acre or basal area per acre, based on the square of the spacing (Cottam and Curtis 1949), yielded quite obviously skewed distributions (Figures 3 and 4). The form of the curve in Figure 4 suggested the logarithmic transformation in Figure 5, which appears to yield a normal distribution, a hypothesis supported at the 5% level by the chi-square test of goodness of fit.

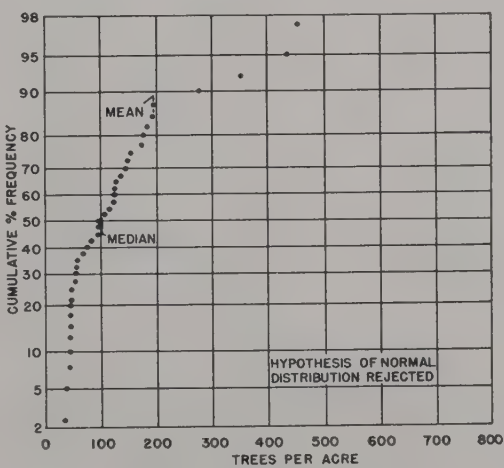

FIG. 3. Cumulative distribution of sample numbers of trees per acre on probability paper, not approximating the straight line of a normal distribution; data from random pair sampling of buckeye-basswood-sugar maple type, 1953 (the fortieth point is at infinity in this and the following figures).

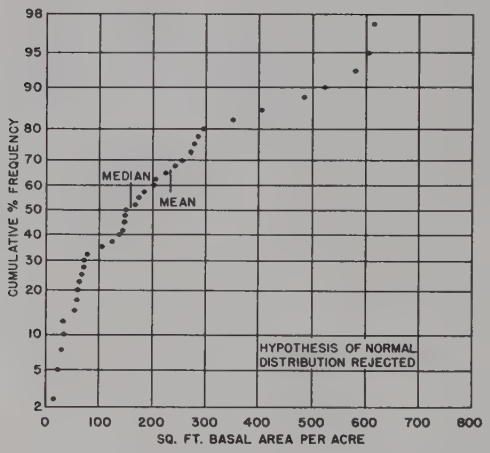

FIG. 4. Cumulative distribution of sample basal area in sq. ft. per acre on probability paper, not normally distributed; data from random pairs as in Figure 3.

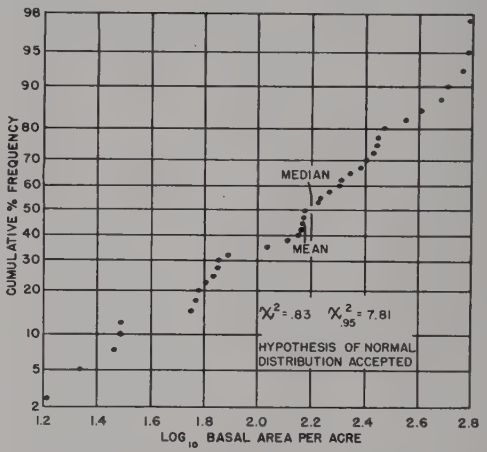

FIG. 5. Logarithmic transformation of Figure 4 on probability paper, approximating the straight line of a normal distribution.

This transformation therefore made possible the application of conventional statistical procedures based on normal distribution (Shanks 1953). The resulting stand estimate from random pairs agrees quite satisfactorily with estimates from the other sampling methods (Table VI).

TABLE VI. *Stand estimates in sq. ft. basal area per acre, based on different methods of sampling and computation, buckeye-basswood-sugar maple type, Great Smoky Mountains, 1953*

	Lower 95% confidence limit	Central tendency	Upper 95% confidence limit
Plots, tenth-acre (25)			
mean	150.5	171.4	192.3
median	131.3	162.5	212.1
Plotless, variable-radius (40)			
mean	121.8	165.8	209.8
median	145.6	168.0	179.3
Random pairs (40)			
mean, untransformed data	.....	233.7	.....
mean, transformed data	106.9	147.8	204.2
median	108.6	159.0	241.0

Species frequency

Species frequencies are strongly influenced by sample size (Gleason 1929, Cain 1932, 1943a, Penfound 1945) and frequencies from random pair samples were quite low, differing markedly from those derived from other types of samples (Table VII, as well as in Table I, item 7). Only by translating them into "relative frequencies," based on total frequency points and totalling 100% for all species (Curtis and McIntosh 1950), can the bias due to sample size be eliminated, and the effectiveness of different sampling methods as a measure of species dispersion be compared. Such a comparison is made in Table VIII, which shows reasonable agreement among the different sam-

TABLE VII. *Frequencies (% of samples in which species occurs) based on different sampling methods, buckeye-basswood-sugar maple type, Great Smoky Mountains, 1953*

Species	Plots, tenth-acre (25)	Variable-radius plotless (40)	Random pairs (40)
Aesculus octandra	92	97.5	35
Acer saccharum	92	90	45
Tilia heterophylla	76	87.5	25
Halesia carolina	48	37.5	17.5
Tsuga canadensis	36	20	2.5
Betula lutea	32	22.5	2.5
Quercus rubra	24	52.5	7.5
Carya glabra	24	30	7.5
Liriodendron tulipifera	8	5	0
Acer rubrum	4	12.5	2.5
Fraxinus americana	4	12.5	0
Ostrya virginiana	4	5	2.5
Juglans nigra	4	5	0
Carya cordiformis	4	2.5	0
Fagus grandifolia	4	2.5	0
Acer spicatum	4	0	0
Cornus alternifolia	4	0	0
Magnolia fraseri	0	2.5	0
Summary by classes— No. of species			
0-20%	9	8	7
21-40%	4	3	2
41-60%	1	1	1
61-80%	1	0	0
81-100%	2	3	0
Total	17	15	10

pling methods. In the light of the data of Table VII, and those of the investigators cited above, the agreement of frequencies cited by Cottam and Curtis (1949: 103) is unusually close, and suggests a simple and uniform stand with wide spacing. It is believed that the sample-size relationship reported here for the Appalachian vegetation is the more general situation, and that the use of relative frequency will usually be advisable for comparative purposes, as recognized by Curtis and McIntosh (1950) and employed by the Wisconsin group in later studies (Curtis and McIntosh 1951).

Concluding Discussion

Variable-radius plotless sampling

It is evident that variable-radius plotless sampling has certain advantages over conventional sampling methods: (1) it is much more efficient; its yield of information per man-hour is several times as great; (2) it is much more adaptable to use by a single person; less elaborate preparation is required and it may therefore be appropriately used as a reconnaissance survey procedure as well as in more detailed studies; (3) its sample data appear to be normally distributed and conventional statistical analysis is therefore directly applicable; this appears not to be true for random pairs when used as unit samples, and is questionable for small plot samples. Although they are not standard frequency data, the frequency data which are available from this method express the frequency of effective contribution to the stand. Only those minor species which are consistently of small size tend to have values lower than their conventional plot frequency values in the stand, such as serviceberry, mountain holly, and mountain ash in Table I. For the major species, the frequency values from the variable-radius samples are considered a reasonable substitute for conventional frequencies, and they are so used in constructing the phytographs of Figure 1.

Table VIII. *Relative frequencies of important species from Table VII (% of total frequency points) by different sampling methods*

Species	Tenth-acre plots (25)	Variable-radius plotless (40)	Random pairs (40)
Aesculus octandra	19.9	20.3	23.7
Acer saccharum	19.9	18.8	30.5
Tilia heterophylla	16.5	18.2	17.0
Halesia carolina	10.4	7.8	11.9
Tsuga canadensis	7.8	4.2	1.7
Betula lutea	6.9	4.7	1.7
Quercus rubra	5.2	11.0	5.1
Carya glabra	5.2	6.2	5.1

Little added effort is required to tally the plotless samples by 6-inch diameter classes. This results in a tally of stand per acre in each diameter class, from which may be computed the average number of trees of such size per acre. Figures so derived may be combined into a reasonable substitute for conventional density data, as in Table IV.

It is concluded that the variable-radius plotless sampling of Bitterlich as described by Grosenbaugh is an adequate and extremely efficient method. Conventional data or reasonable substitutes for them may be derived from it and confidence limits may be established by standard statistical methods.

Random pairs

Two-tree samples ("random pairs") can also be effectively used as a basis for characterizing a forest stand. They yield information on species composition (per cent of total stems for each species), stand per unit area (number of trees or basal area per acre), and species dispersion (frequency in a series of samples). However, samples obtained by this method have certain characteristics which should be recognized before vegetation inferences are drawn: (1) a tendency to underrepresentation of species which are clumped, such as basswood; (2) a skewed distribution of data on tree number or basal area per acre, which is the extreme case of general small sample bias; and (3) the influence of the extremely small sample size on species frequency.

The biased data on basal area per acre may be transformed logarithmically into an approximately normal distribution, making possible the application of conventional statistical analyses. Stand estimates from random pairs based on transformed data, or on the median, agree satisfactorily with estimates from plot or variable-radius sampling, while those from untransformed data do not. The effect of small sample size on species frequency may be satisfactorily eliminated by the use of relative frequency.

Conclusion

While a more rigorous test of both plotless sampling methods is still desirable, in an area where a complete inventory of the vegetation is available, the data at hand are encouragingly consistent, and the following conclusions appear to be warranted. Both of the plotless methods are rapid as compared with plot sampling and are adaptable for use in rapid reconnaissance. Both are operable by one person at a reasonably efficient level, but it is believed that maximum efficiency would be achieved by a two-man crew in either case. Both are susceptible to statistical measures of varia-

bility, although such treatment has not been customarily used with the random pairs. In this connection, the probable usefulness of the median and its confidence intervals should be further explored.

Neither of the two plotless methods adequately samples the inferior layers or inferior size classes in the forest stand. The type and intensity of supplementary collection of data, whether by plot, line, series of points, or simply a presence checklist, must be decided with these methods just as with any other forest sampling method, and the decision will be influenced by both objective and time available.

When faced with a choice of method, the writer would choose for reconnaissance sampling the variable-radius method described by Grosenbaugh. The greater yield of information per point results in more information per man-hour in the field, and the simpler computational procedure means fewer hours of follow-up analysis. The greater amount of information per point also means that the method is more useful in the study of local topographic vegetation pattern. On the other hand, the random pairs method, or a modification of it, would be most useful where attention was focused primarily on species association or on details of tree spacing in a forest stand.

Summary

Two plotless sampling methods were compared with each other and with conventional plot sampling in both high-altitude spruce-fir and mid-altitude buckeye-basswood-sugar maple forest types in the Great Smoky Mountains. Both were superior to plot sampling in yield of information per man-hour, but random pairs required transformation of data or use of order statistics before valid confidence limits of stand estimates could be established. The sampling methods all differed from each other in the precise type of information provided, but if handled appropriately, all three methods led to very similar vegetation inferences. It was concluded that the Bitterlich variable-radius method using an angle-gauge was superior for reconnaissance sampling in the types studied, but that a method based on random pairs would be superior for certain kinds of studies of stand structure.

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FECUNDITY OF ENTOMOPHAGOUS INSECTS UNDER MASS CULTURE, AN EFFECT OF ENVIRONMENTAL RESISTANCE[1]

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INTRODUCTION

The mass culture of entomophagous insects for use in biological control work involves the propagation of such insects at high population densities in artificial environments under exacting procedures of handling. With populations under these conditions, as in the field, environmental resistance is the principal factor limiting production. (A population consists of two or more individuals of a species, each of which may influence the activity of another.)

The purpose of this paper is to outline the types of culture methods that have been developed, and to analyze the fecundity of propagated species in relation to environmental resistance and methods used.

There are a number of species of entomophagous insects for which more or less standardized methods of mass culture have been developed. Some of these species, and the food material involved in their production, are as follows: *Cryptolaemus montrouzieri,* in production for the past 30 years, using mealybugs on potato sprouts (Smith and Armitage 1931); *Trichogramma evanescens,* in production for the past 26 years, using eggs of the Angoumois grain moth (Flanders 1930); *Leptomastix dactylopii,* in production for the past 18 years, using mealybugs on potato sprouts (Flanders 1949); *Metaphycus helvolus,* in production for the past 14 years, using black scale on potato sprouts (Flanders 1949). Within the past 13 years *Microplectron fuscipennis* has

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FIG. 1. Insectary room containing 50 stacks of wire trays, each tray holding 20 pounds of potatoes infested with tuber moth larvae that have been subjected to parasitization by *Macrocentrus ancylivorus* Roh. Infestations of equal age are on separate stands. When the White Rose variety of potato is used, 75 to 80 per cent of the host larvae are parasitized, the average pound of potatoes yielding 200 adult parasites; when the Russet variety is used, parasitization is 65 to 75 per cent, the average pound yielding 170 adult parasites (Finney, Flanders, and Smith 1947).

FIG. 2. Insectary room containing stacks of metal boxes, each containing a tray of potatoes. Infestation of potatoes with tuber moth larvae and their exposure to parasitization takes place in these boxes. The inoculum for each box consists of five *Macrocentrus* females per pound of potatoes. The exposure period is from 3 to 4 days. The life cycle averages 23 days.

been mass-produced on cocooned larvae of European spruce sawfly (Miller 1940); *Macrocentrus ancylivorus,* on feeding larvae of potato tuber moth (Figs. 1, 2); *Chrysopa californica,* on the larvae of potato tuber moth (Finney 1948); and *Aphytis chrysomphali,* on red scale infesting grapefruit (Flanders 1951).

The insect populations used in most of these culture operations were very large, since they were propagated for release over large areas of agricultural crops. The annual production of each of the entomophagous species now under mass culture ranges between 1 and 40 million adults. As a rule, culture operations are carried on at a temperature of 80° F. and a relative humidity of 55 per cent. The immediate purpose of such culture operations is the production of the maximum number of female-producing females of the entomophagous species in a minimum period of time.

Within the limits set by the housing facilities and by the biological characteristics of the species concerned, the higher the insect population densities, the greater the production per unit of space and of time. This occurs in spite of the fact that an increasing population density causes a decreasing fecundity per individual, as measured by the mature progeny of the average parent. Because of this relation between population density and fecundity, the measure of operational efficiency in mass culture is the total number of entomophagous females produced per unit of space, rather than the total number produced per parent (Flanders 1949). Since space is limited, maximum efficiency in handling of food chain (food base and host or prey) and in production of parasite or predator per unit of time requires the maximum rate of culture replacement. Species having the highest rate of reproduction and utilizing the smallest amount of food per individual are produced in the greatest numbers.

Inherent Fecundity versus Actual Fecundity

Because of environmental resistance, the maximum number of progeny attainable per female (the inherent fecundity or reproductive capacity of the species) is rarely if ever realized under mass culture. As Chapman (1931) has pointed out, the inherent fecundity of a species is realized only in an environment in which all the environmental factors are at the optimum for reproduction. Such conditions do not occur in any population, however, since one individual affects the behavior pattern and action rate of another.

The total actual fecundity of an individual member of a population is a function of population density. Such fecundity is the average number of progeny completing their development per female parent, and it equals the inherent fecundity minus the effects of environmental resistance. "Inherent fecundity" as used herein is synonymous with "intrinsic rate of natural increase" (Birch 1948) if the latter phrase signifies the total increase per individual under specified physical conditions in an unlimited environment where the effects of increasing density do not need to be considered. The situation as thus defined, however, is rarely if ever natural.

Although the inherent fecundity of a species, or its approximation, is not in itself indicative of the actual fecundity that may be attained under mass culture, it provides a basis for comparing the adaptability of various species to mass culture and for measuring the environmental resistance to which they are subject. The measurement of inherent fecundity in species adapted to artificial environments necessitates the isolation of the individual gravid female (and of each of her offspring in nongregarious species) under environ-

mental conditions that are free of mortality factors and that are optimal for the development of the entire complement of oogonia, for oviposition rather than for ovisorption, and for the development of progeny. It is considered that the maximum number of progeny per female obtained from females thus isolated adequately represents the inherent fecundity of the species.

On the basis of these criteria, the records of the known cases of mass culture show that actual fecundity ranges from approximately 50 per cent of the inherent fecundity, as with *Microplectron fuscipennis,* to approximately 6 per cent, as with *Macrocentrus ancylivorus* (Finney *et al.* 1947; Miller 1940).

The inherent fecundity of a species such as the biparental sawfly parasite, *Microplectron fuscipennis,* is readily ascertained, since it develops gregariously and the female, when isolated in a glass vial with a single host individual, deposits her entire complement of eggs (approximately 65) within a 5-day period, with the single host providing all the nutriment needed for the complete development of the entire brood (Wilkes 1947). Under mass culture with bisexual inocula its increase measured in adult progeny is about thirtyfold (Miller 1940).

The inherent fecundity of a uniparental parasite such as *Aphytis chrysomphali* is especially difficult to ascertain, since it may not oviposit readily when isolated in small units, may absorb more eggs than it oviposits, must feed on certain stages of the host in order to complete the development of its eggs, may destroy by mutilation the host upon which it has oviposited, and may deposit more eggs on a host than can complete their development. Under mass culture its increase is about threefold (Flanders 1951).

In the mass culture of the biparental parasite *Trichogramma evanescens* on eggs of *Sitotroga cerealella,* the actual fecundity is about 10 per cent of the inherent fecundity of the female. The increase obtained under mass culture is about sixfold (Flanders 1930).

In the mass culture of the biparental coccinellid *Cryptolaemus montrouzieri,* the actual fecundity is about 80 offspring per female (Smith and Armitage 1931). This is about 50 per cent of the inherent fecundity observed by E. J. Brannigan (unpublished notes). Under mass culture the increase based on the use of adults of both sexes is about fortyfold.

When the endoparasite *Macrocentrus ancylivorus,* whose inherent fecundity is about 500 per female, is mass-propagated on the potato tuber worm, its increase is thirty- to fortyfold, parasitization varying from 75 to 80 per cent when the host is in fresh White Rose potatoes and from 30 to 45 per cent when its host is in old Russet potatoes. This difference is an effect of different types of distribution of the host in the different types of potatoes.

The reduction of fecundity in the mass culture of these species is an effect of mutual destruction (cannibalism, superparasitism, and mutilation) and of mutual depression of the amount and rate of oviposition and of development. As population densities increase, additional reductions in fecundity may result from increased incidence of disease and from competition by pest insects. Fortunately, under mass culture it is possible to minimize the influence of certain of these adverse factors by completely utilizing the food material (host or prey) at a high rate and thus effecting a rapid turnover of populations.

The actual fecundity of an entomophagous species at low population densities gives no indication of its actual fecundity at high densities or densities at which maximum production per unit of space or of time is economically attained.

The entomophagous inoculum should be fully utilized in a minimum of time commensurate with efficient reproduction. As a rule, the shorter the period of exposure of host or prey to a given inoculum, the smaller the amount of loss due to cannibalism, superparasitism, disease, and competition by pest insects. A rapid turnover of material not only minimizes the adverse effects of population densities, but also increases the number of individuals produced per unit of space, as well as of time. Rapid turnover of material, therefore, is usually a critical factor in economy of production. This factor, within the limits set by the biology of the species, determines the method employed to bring the populations of host and parasite and of prey and predator into contact.

General Methods of Mass Culture

Under conditions of mass culture, the behavior patterns of the species involved and the environmental resistance to which they are subjected have brought about the use of three general types of culture methods for bringing parasite and predator populations into contact with their respective host and prey populations. These methods are (1) the periodic-contact method, (2) the limited-contact method, and (3) the continuous-contact method.

In the use of the periodic-contact method, successive populations of host or prey are briefly exposed to a parental (parasite or predator) stock population which is permanent in number of individuals; the stock being maintained by periodic addition of inocula. The progeny populations of

the latter are isolated while in immature stages. Examples are *Aphytis* spp. propagated on California red scale (Flanders 1951) and *Dibrachys cavus* propagated on potato tuber worm (Doutt and Finney 1947). The host population in each of these cases is placed within the sphere of action of the parasite population for only a short period.

In the use of the limited-contact method, a short-lived population (inoculum) of a parasite or predator is introduced into a host or prey population. The maximum actual fecundity of the former is attained only by providing an adequate supply of host or prey. The parasite or predator progeny in completing its development should utilize practically all the host or prey population. The entomophagous inoculum may or may not live long enough to deposit its full complement of eggs. Examples are *Macrocentrus ancylivorus* propagated on potato tuber moth (Finney *et al.* 1947), *Microplectron fuscipennis* propagated on European spruce sawfly (Miller 1940), and *Cryptolaemus montrouzieri* propagated on mealybugs (Smith and Armitage 1931).

In the use of the continuous-contact method, host and parasite populations are reared together in the same production unit and thus are continuously in contact. This unit is maintained by stocking it regularly with the food base in amounts that will be almost completely utilized by the host population. It is essential that a small portion of the host population infesting the food base be outside the oviposition range of the parasite, this portion being sufficient to maintain the population of adult hosts needed to infest properly the regularly added food base. The adult parasites are removed daily, except the few needed to parasitize the available hosts. In this type of culture, which is without rapid turnover of material, extreme care must be taken to prevent contamination with competitive organisms, and to reduce the incidence of disease. An example is *Idechthis canescens* on *Ephestia kühniella* (Flanders 1948).

The method selected for the mass culture of an entomophagous species depends in part on the developmental relation of that species with its host or prey, the conditions that stimulate egg deposition, and the period of host or prey susceptibility to attack.

Actual Fecundity versus Amount of Population Increase

The contact methods affect the actual fecundity of the entomophagous species and the amount of increase obtained, either per inoculum or per unit of time. Under conditions of mass culture the actual fecundity of a species is the total progeny per parent female, whereas the amount of increase is the number of times the progeny population exceeds the parental population, regardless of the sexuality of the latter. With unisexual populations of *Aphytis chrysomphali,* actual fecundity equals the amount of increase, which is threefold (Flanders 1930). In the mass culture of a biparental species it may or may not be economical to have the inocula entirely female. This depends on the biology of the species and the ease with which the sexes can be segregated. With *Macrocentrus ancylivorus* for example the activity of the male interferes with the oviposition of the female, so only females are included in the inocula. The amount of increase in this particular species is measured when the progeny is in the cocoon stage.

With Hymenoptera that are biparental in reproduction, the sex-ratios normally may be highly variable without differential mortality being involved (Flanders 1942). If the sex-ratio of parasitic inocula is highly variable, the amount of increase in relation to the actual fecundity may also be highly variable. The factors causing the production of males in place of females constitute a highly detrimental phase of environmental resistance (Flanders 1945).

The minimum total amount of increase to be expected from an inoculum under economical mass culture happens to be about equal to the number of eggs the average female is inherently capable of producing per day. This is approximately the amount of increase that has been obtained with *Aphytis chrysomphali, Trichogramma evanescens,* and *Macrocentrus ancylivorus.*

For the most economical mass culture it is essential to utilize the parental stock to its full capacity. As a rule, the periodic-contact method, a continuous succession of host or prey populations briefly exposed to a permanent parental (parasite or predator) stock population so that environmental resistance is at a minimum, is the most likely method of obtaining the maximum increase possible under mass culture.

Summary

The culture methods developed during the past 30 years for producing entomophagous insects *en masse* are of three general types, namely, periodic-contact, limited-contact, and continuous-contact.

The fecundity of the species may be manifested in three ways based on the increase either per female or entire inoculum. These are designated inherent fecundity, actual fecundity, and amount of increase. Culture methods and fecundity are discussed in relation to environmental resistance, which accounts for the differential between inherent fecundity and actual fecundity.

The measure of operational efficiency is the

number of entomophagous females produced per unit of space; the measure of production efficiency is the number produced per unit of time. The minimum amount of total increase per inoculum to be expected under economical production is about equal to the average number of eggs produced per female per day. In known cases of mass culture, amount of increase has ranged from threefold to fortyfold.

The actual fecundity to be expected under mass culture ranges from approximately 6 to 50 per cent of the inherent fecundity, the decrease in fecundity being a measure of the environmental resistance.

The detrimental effects of environmental resistance are minimized in part by rapid utilization (turnover) of material.

In the culture of hymenopterous parasites, the factors that cause the production of males in the place of females contribute to environmental resistance.

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REGULATORY MECHANISMS IN HOUSE-MOUSE POPULATIONS: THE EFFECT OF LIMITED FOOD SUPPLY ON AN UNCONFINED POPULATION

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There have been several recent studies on factors involved in the development and maintenance of wild house-mouse (*Mus musculus*) populations (Young *et al.* 1950; Strecker and Emlen 1953). The present study is part of this series and reports the development of two populations under conditions of limited daily food supply, with means of egress from the area available. I would like to thank Dr. J. T. Emlen, Jr., Department of Zoology, University of Wisconsin, and Dr. Howard Young, Department of Biology, Western Illinois State College for their frequent advice and help in the study. The work was done at the University of Wisconsin as part of a thesis project for a doctoral dissertation. It was supported by a grant from the National Institutes of Health.

Methods

Two colonies of house mice were used in this study, each being established by releasing wild adult house mice into a room previously without mice. This room was on the sub-basement level of a University of Wisconsin building. It had a floor area of about 2600 square feet, and contained two fans used in ventilating the building. Numerous pipes and a large amount of stored material, including jars and crocks, tables, lumber, asbestos pipe casing, and other miscellaneous materials stacked at one end provided cover for the mice (Fig. 1). The remainder of the room was rather bare except for the fans, a large radiator, several motors and pipes. The temperature of the room was about that of outside temperature in summer, and was quite warm in winter. Means of egress from the room consisted of obscure and undetermined pathways, evidently along the ventilating shafts which ran throughout the building.

There was no food available in the room other than that provided by the investigator, and hence the food consumption could be determined by

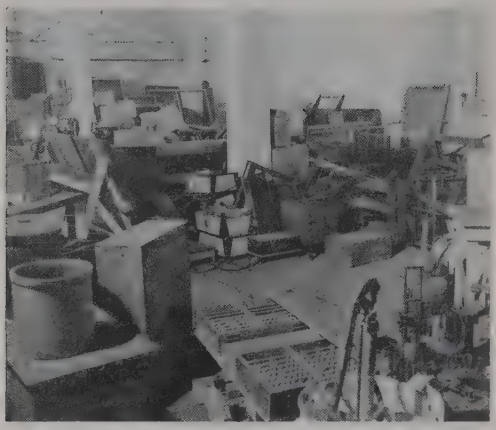

FIG. 1. Photograph of one end of the room used for the mouse colonies, showing the general type of cover available.

measuring the amount eaten out of that supplied. The food consisted of a mixture of equal parts of rolled oats, ground corn, ground wheat, powdered commercial rat pellets, and one fourth part of powdered meat scrap, with some salt and cod liver oil added. This mixture was divided into four portions, placed in shallow pans at different locations in the room. Water was supplied in excess at four locations also.

Two separate populations were studied in the room, one from August to December, 1948 (hereafter referred to as the '48 colony) and one from January to December, 1949 (hereafter referred to as the '49 colony). Both were established by releasing five male and five female adult wild house mice, each individually marked by toe clipping. The population growth was followed by determining the amount of food consumed in twenty-four hour periods. This method has been found to give a satisfactory index of population growth in confined populations of known size. (Strecker and Emlen 1953). In addition, live-trapping with wooden box traps was conducted at weekly intervals. All mice captured were individually marked by toe clipping. This yielded some further information on growth, reproduction, and movements by the individuals. At the conclusion of each of the studies, all mice were removed by placing a large number of baited snap-traps in the room and removing all food.

Population Growth

As previously mentioned, the populations were established by releasing 5 pairs of adult mice; the growth of the populations was measured in terms of total daily food consumption, since it was not possible to capture all individuals at any one time.

The curves of the average daily food consumption for each weekly period are given in Figure 2.

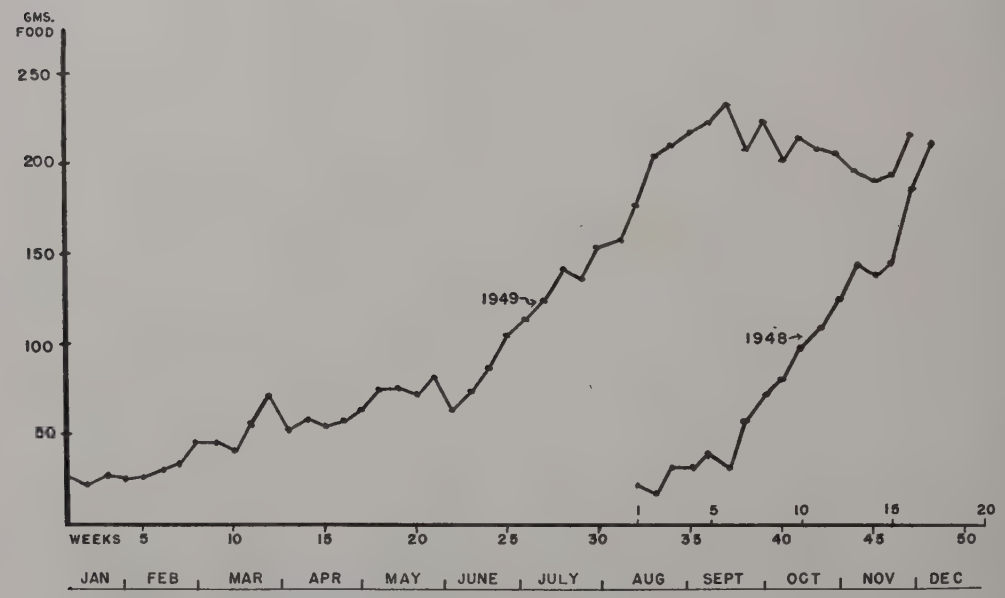

FIG. 2. Graphs of average daily food consumption for each week in the '48 and '49 populations, excluding food consumption on days when live-trapping was conducted.

The '48 colony was established on August 9. The first indications of reproduction were obtained on September 25, when young mice two or three weeks of age were captured in the live-traps. The food consumption showed a steady increase from this time on. The total daily food supply was 500 grams, so that at the conclusion of the study in early December, there was still a great excess of food present.

A total of 48 mice were live-trapped and marked during the '48 study. Of these, 34 (71%) eventually died within the colony room, either being found dead, or caught in the final snap-trapping. Nine (19%) were recovered outside the colony room, and 5 (10%) were not located at the time of their death. In the snap-trapping in the room at the conclusion of the study, a total of 76 mice were caught, 33 of which were marked individuals.

The '49 colony was established on January 7, 1949. Young mice were captured first on February 19. This colony got off to a somewhat slower start than the one in '48 but by the twelfth week had begun a rapid growth comparable to the increase of the '48 colony. However, during the thirteenth week (early April) five adult mice from the population were accidentally killed. Three of these were pregnant females, one was a lactating female, and one an adult male. This was a severe loss to the population, as indicated in the decided lag in food consumption for the next ten weeks. By mid June the population had again begun to increase rapidly, and the food consumption curve in the following 11 weeks closely paralleled that of the '48 population.

For the '49 population, only 250 grams of food were supplied daily. By late August nearly all of this daily allotment was being consumed. The irregularity of the remainder of the curve was related to fluctuations in the population due to egress, as will be discussed later. A total of 234 mice were live-trapped and marked during this study. Of these, 79 (34%) died in the colony room, either being found dead at various times during the study or being caught in the final snap-trapping. Ninety-one (39%) were recovered outside the colony room, and 64 (27%) were not recovered at death. In the snap-trapping at the conclusion of the study, 87 mice were captured, 59 of which were marked individuals.

It is evident, then, that the two populations in their period of maximum growth show very similar curves, based on food consumption. The 1948 population developed rapidly, and was concluded while still in a period of rapid growth, with food present in excess. The '49 population had a slow start, but once under way, its growth paralleled that of the '48 population. However, nearly complete consumption of food was reached some three months before the conclusion of the '49 colony. This population then evidently remained fairly stable for three months at a level slightly below total food consumption, with surplus individuals leaving the colony, as will be discussed below. As a result, no actual food shortage ever developed, and there was no indication of any change in rate of reproduction. Young mice recently out of the nest were caught frequently up to the conclusion of the study. Of the 87 mice recovered in the final snap-trapping in December, 17 (20%) were immature mice under ten grams in weight, and of the 23 females weighing over 14 grams, 13 (57%) were visibly pregnant on gross autopsy.

Population Dispersal

Mice were recovered outside the colony by keeping snap-traps set at all times throughout the upper floors of the building. It would have been preferable to use live-traps and release all mice for further observations, but this was not feasible because the recoveries were usually in offices or laboratories. It therefore cannot be finally stated whether these movements represented true egress or extensive foraging excursions. The length of the movements makes the latter unlikely however, since under somewhat similar conditions it has been shown the normal range of house mice averages about twelve feet (Young *et al.* 1950). There was even one litter born at a location six floors away in the present study. This suggests that these moves were of a more permanent nature than mere foraging excursions or range extensions.

Time of Egress. The time of egress of an individual could be taken either as the date of its last live-capture in the colony room, or as the date of its recovery outside the room in the snap-traps. Obviously the correct time lies somewhere between the two.

In the '48 study only 9 marked mice were caught outside the room, scattered over a period of several months. In the '49 study, 91 marked mice were captured outside the room. Using the time of their last live-capture in the colony as the assumed day egress occurred, 21 were recovered in the seven months from January to July, and 70 in the four months from August to November. Using the time of their snap-capture outside the colony as the assumed day egress occurred, only 6 were captured in the period from January to July, and 85 in the period from August to November. This latter method is felt to be more nearly correct, since the snap-traps outside were kept set and baited at all times, and in most places of cap-

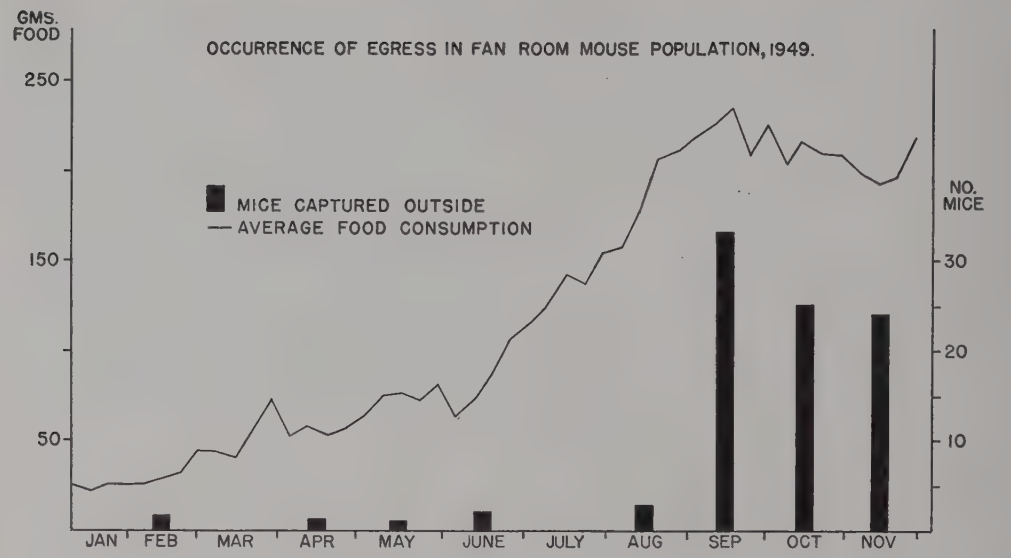

FIG. 3. The time of egress of marked mice based on capture outside the colony in 1949. Also shown is the average food consumption in the colony during the same period.

ture there was no food available, while mice caught appeared quite healthy. Also it has been found that mice frequently will be present for long periods of time without being recaught in live traps (Evans 1949; Young *et al.* 1950; Young *et al.* 1952). A monthly breakdown of numbers captured outside the colony in 1949 is given graphically in Figure 3, along with the graph of food consumption. It can be seen that as total food consumption was approached, there was a rapid increase and a maintained high level of egress, so that complete consumption of the daily food supply was never reached.

Ages and sex of mice in egress. A sufficient number of mice were caught in egress from the '49 population to give some picture of the age and sex of mice involved. Those animals caught outside the colony were separated by weight classes, a rough indication of age in healthy individuals. These data are summarized in Table I, and indicate that all mice except the very youngest joined in the egress. The smallest female captured outside weighted 10.1 grams, with a body length of 74 mm; the smallest male weighed 12.6 grams with a body length of 75 mm. All of the 44 females but two had perforate vaginae, and 12 of them were visibly pregnant on gross autopsy. All of the 47 males but one had a testis length of 5 mm, or more, although 12 showed no seminal vesicle enlargement. Thus egress from this colony involved both subadults and adults, with the sexes being about equally represented.

TABLE I. *The size and sex of mice caught in egress from the '49 population.*

	Weight Class			
	10.1-15 gm.	15.1-20 gm.	20.1+gm.	Total
Males	12	27	8	47
Females	15	18	11	44
Total	27	45	19	91

Effect of egress on the remaining population. Both of the colonies were exterminated by intensive snap-trapping at the end of the experiments. The '48 population had run for four months, was increasing rapidly with food still in great surplus, and had had only a small amount of egress occurring. The '49 population had run for 11 months, had been limited by daily food supply for about 3 months, and had had egress occurring at a high rate during the final 3 months. The comparison of these populations is of interest, then, to see if the limited food and high rate of egress in 1949 had caused any noticeable difference in the composition or rate of reproduction of the colony. The data are summarized in Table II, and show no differences of any statistical significance. Both colonies had a representation of mice from all age classes, and both had high rates of reproduction. No young mice still in the nest were found, and such litters are not included in any of the data.

TABLE II. *Comparison of the '48 and '49 population samples recovered by intensive snap-trapping in the colony room at the conclusion of each study.*

Weight Class	1948 No.	1948 Per cent	1949 No.	1949 Per cent
10 gm. or less	25	34	17	20
10.1-20 gm.	39	53	52	59
20.1 gm. or more	10	13	18	21
Total	78*		87	
Sex ratio ♂♂: ♀♀		42:58		48:52
Females pregnant	9 (21%)		13 (29%)	

*Including 4 adults on which no weights were obtained.

DISCUSSION

The factors affecting the dynamics of development, maintenance, and dispersal in animal populations are very complex, but by examining individual factors, it is possible to get some insight into the role of those factors and their effects on the population. Young *et al.* (1950) found that free-living house mice under near-optimal conditions of food and cover were very localized in their movements, and evidence of any egress was slight. Strecker and Emlen (1953), using artifically established populations of wild house-mice, found that a limited daily food supply resulted in an abrupt cessation of all reproduction when total food consumption was reached and egress was prevented, although all adult mice in the colony showed satisfactory weight maintenance and viability. The populations described in this study were similar to the latter in having a limited daily food supply, but differed in having paths of egress from the colony available. Here the reaction was quite different, and as a daily food shortage approached there was a great increase in the amount of egress from the colony so that no actual food shortage ever developed. Reproduction in the colony continued at apparently normal rates. This situation resulted in a wide and continuous dispersal of the mice through the available adjacent area. These results indicate the importance in rodent control of thoroughly reducing populations before habitat destruction and cleaning up is begun.

SUMMARY

Populations of wild house-mice were established in a large room with suitable cover, previously unoccupied because of the absence of any food supply. Water was supplied in excess, but limits were established on the daily supply of food. In the first colony, where food was in excess at all times, the animals got along well, with a rather steady low rate of egress from the colony over the four months' period. In the second colony less food was supplied, so that after 8 months total daily consumption was approached. At this time egress began to occur at a high rate, and continued for 3 months, until the study was concluded. Reproduction too continued at a good rate, and at the termination of the study the general composition and the reproductive activity of the population were essentially like that of the first colony. This is in contrast to the abrupt cessation of the reproductive activity in a similar colony from which egress had been prevented (Strecker and Emlen 1953).

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AN INTERPRETATION OF THE CHANGES IN TYPE OF THE POPULATION DENSITY EFFECT UPON THE OVIPOSITION RATE

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INTRODUCTION

It is generally accepted that the types of the population density effect of insects upon their oviposition rates may roughly be classified into the following two: one is the monotonously decreasing type as shown schematically in Figure 1 and is usually called the *Drosophila* type; and the other is the so-called Allee type, of which the existence of an optimum density point is characteristic, as shown in Figure 2. In these figures, the ordinate axis denotes the average rate of oviposition (number of eggs deposited per day

per female adult), and the abscissa the population density (size) of adult insects. As was demonstrated by Utida (1941) with an experimental population of the azuki bean weevil, *Callosobruchus chinensis* (L.), however, there is an intermediate type belonging to neither of these two. Utida's result is shown in Figure 3. Accordingly, it must be considered that the types of the density effect may not be identified so definitely as generally thought, but rather vary characteristically from species to species. Many attempts have been made to interpret such variations in terms of various biological and physical features associated with insect populations, including cannibalism, changes in fecundity and fertility, increase in mortality of adult insects, environmental conditioning, etc.; a concise review has been presented in the introduction of a recent paper of Boyce (1946). Nevertheless, the interpretations hitherto presented are essentially of a qualitative nature, and quantitative considerations of the problem are still scarce in the literature. It is therefore of interest to consider quantitatively what are the major controlling factors for the types of density effect among various parameters associated with population dynamics. There are some experimental facts showing that in some cases, even at constant environmental conditions, the type of density effect of a given insect population is not maintained invariable during the course of a particular experiment, but changes systematically as the period of incubation is prolonged. Such facts were demonstrated with populations of *Tribolium confusum* Duval by Chapman (1928) and especially by Park (1932), who found that the density effect of this insect changed its type from an Allee type to a *Drosophila* one as the duration of rearing was increased. This indicates that the density effect is really a time-dependent property, and suggests the importance of *time* in the quantitative treatments of the population density effect.

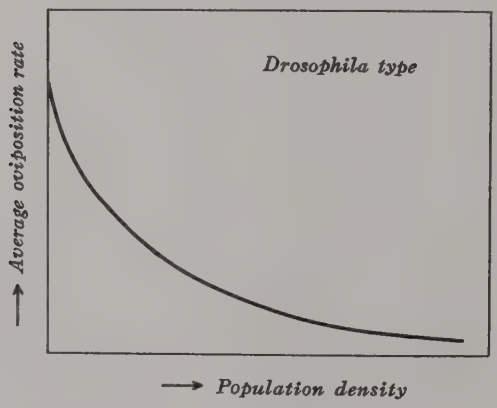

FIG. 1. Schematic representation of the population density effect of the *Drosophila* type.

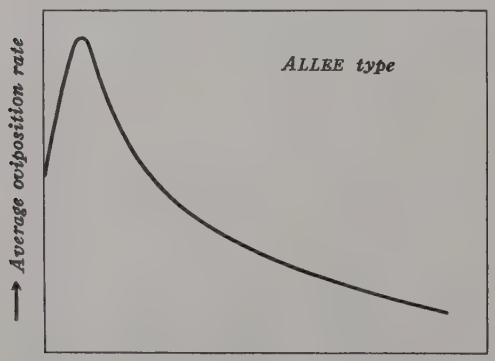

FIG. 2. Schematic representation of the population density effect of the Allee type.

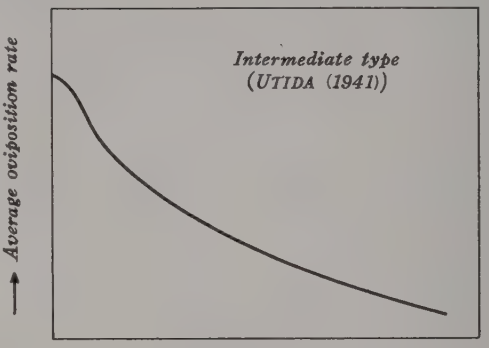

FIG. 3. An intermediate type of population density effect, found by Utida (1941) for an experimental population of the azuki bean weevil, *Callosobruchus chinensis* (L.).

It is the purpose of the present paper to formulate the oviposition process in an insect population based on some simplifying or idealizing assumptions as to the structure of the population, with special reference to the changes in its type as influenced by some interesting parameters appearing in the theory.

MATHEMATICAL CONSIDERATIONS

Suppose that $\frac{1}{2}N$ pairs of parent adults of a given insect species are introduced in a culture medium and deposit their eggs under a constant environmental condition. The present discussion is confined to the period of oviposition, that is, the

interval from the instance at which a first egg is deposited to the time at which the first larva hatches. Let E be the total number of eggs found in the medium at any time t in this period, and let a be the area occupied by a single egg deposited. For the sake of mathematical simplicity, it is assumed that the medium is two-dimensional, that is, it is extended plane-wise with a negligible depth as compared with its surface area. The quantity a must therefore be measured in terms of the fraction of the total surface area of the medium, and its uniformity is also assumed. With these simplifications, we shall here assume that the differential rate of oviposition, dE/dt, is controlled by the following four factors:

(i) the natural (or intrinsic) rate of oviposition, ϵ, of the insect species under consideration at the given environmental condition;

(ii) the number of female adults, $\frac{1}{2}N$, where the sex ratio of the population is assumed to be unity;

(iii) the area available for oviposition at a particular time concerned, which is represented by $1 - aE$; and

(iv) the copulation frequency per female; this is the number of copulations per female per unit time, which is denoted by P.

One might conceive many other factors than the above ones which may affect the differential rate of oviposition, such as reduction of fecundity accompanying the crowding of population, cannibalism, death of adults within the period of oviposition, and race of males for copulation with the females. These factors, however, are not considered in the present simple treatment, because the mathematical introduction of these into the theory results in the appearance of many unknown parameters, thus making it difficult to obtain a clear-cut conclusion of the problem under study. According to a recent paper of Boyce (1946), the effect of cannibalism on the oviposition rate is of a secondary nature, even in the population of *Tribolium confusum* in which the reduction of oviposition rate has usually been attributed to a cannibalism.

With these considerations, we obtain from the assumptions set forth above the following differential equation:

$$\frac{dE}{dt} = k\epsilon NP\,(1 - aE), \qquad (1)$$

where k is a proportionality constant. To integrate this equation with respect to E a further consideration needs to be made for P. It is considered that the copulation frequency is increased with increasing adult density, because the crowding of an adult population results in a reduction of mutual distance between adults, thus giving rise to an increase in number of collisions of males and females per unit time. If the collisions are made entirely in a random fashion, it may be assumed that P is represented by a Gaussian distribution function with respect to the average mutual distance between neighboring adults, r. Namely, we may put

$$P = \exp(-\sigma r^2), \qquad (2)$$

where σ is a constant dependent primarily on the copulation characteristics of the given insect species. Since the culture medium has been assumed to be two-dimensional, r is proportional to $N^{-\frac{1}{2}}$, so that equation (2) may be written

$$P = \exp\left(-\frac{\alpha}{N}\right), \qquad (3)$$

where α is a new constant of a same nature as σ. According to equation (3), the copulation frequency, P, is increased monotonously with increasing N, approaching unity as the population is extremely crowded. This is, however, not always the case, as realized from Crombie's excellent experiments with a population of *Rhizopertha* (Crombie 1942). He showed that P in this population first increases rather rapidly, reaches a maxium, and then decreases gradually with increasing density, and ascribed this result to increased fighting by males for females. In spite of this fact, we shall in what follows employ equation (3) for P, since the influence arising from male fighting is rather difficult to deal with quantitatively. Inserting equation (3) into equation (1) and integrating with the initial condition that $E = 0$ at $t = 0$, we obtain

$$E = \frac{1}{a}\left\{1 - \exp\left[-k\epsilon a e^{-\frac{\alpha}{N}} Nt\right]\right\}. \qquad (4)$$

If we denote by E_* the total number of eggs found in the medium at t_* days after the beginning of rearing, we have

$$E_* = \frac{1}{a}\left\{1 - \exp\left[-k\epsilon a e^{-\frac{\alpha}{N}} Nt_*\right]\right\}. \qquad (5)$$

Defining, as usual, the average rate of oviposition, R, by

$$R = \frac{E_*}{\frac{1}{2} Nt_*}, \qquad (6)$$

it follows from equation (5) that

$$R = \frac{2}{aNt_*}\left\{1 - \exp\left[-k\epsilon a e^{-\frac{\alpha}{N}} Nt_*\right]\right\}. \qquad (7)$$

Putting, for the sake of simplicity,

$$\frac{Ra}{2} = Z, \qquad k\epsilon a = \beta, \tag{8}$$

equation (7) can be put in the form:

$$Z = \frac{1}{Nt_*}\left\{1 - \exp\left[-\beta e^{-\frac{\alpha}{N}Nt_*}\right]\right\}. \tag{9}$$

Since Z is proportional to R, we shall hereafter refer to Z as the average rate of oviposition.

Discussion

Equation (4) represents the increase in egg number as a function of time, that is, it is a mathematical expression of the oviposition process. It follows at once from the form of this equation that the process follows an exponential curve, as has been well established by a number of experiments with various kinds of insects. Equation (9) gives the average rate of oviposition as a function of the population density of adult insects, with parameters of t_*, α, and β. The main interest of the present paper is to examine this functional relation between Z and N in regard to the types of population density effect as illustrated in the introduction of the paper.

The effect of t_* manifests itself as a time-dependency of the type of density effect, so that the investigation of this effect is interesting with reference to the experimental results obtained by Chapman and/or by Park for *Tribolium confusum* populations. From equation (3) it is realized that larger values of α result in lower values of the copulation frequency as compared at same values of N. Therefore, the study of the effect of α enables us to inspect what change occurs in the type of density effect according to differences in the copulation tendency of insects. The parameter β is not connected with factors of particular interest to the present consideration, and also, as is readily understood from equation (9), its magnitude does not have an essential influence upon the shape of the Z *vs.* N plot. For these reasons, we shall here confine ourselves to the discussions of t_* and α.

First, with fixed values of α and β, a family of the Z *vs.* N plot was calculated for several values of t_*, and is plotted in Figure 4. It is seen that the resulant curves all resemble the schematic curve of the Allee type as shown in Figure 2. However, with increasing t_*, the optimum density point at which Z reaches a maximum value is shifted toward lower densities, and beyond a certain critical value of t_*, it enters the region of densities less than 2, which is really the smallest possible value of population density. In such a

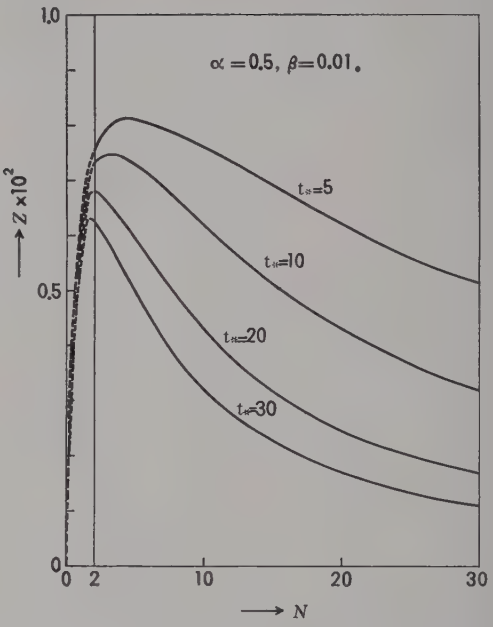

Fig. 4. Effect of the period of incubation on the shape of the Z *vs.* N plot, where Z is the average oviposition rate and N is the population density.

situation where t_* is greater than the critical limit, the plot should appear to the observer as a curve of the *Drosophila* type. This result indicates that, so far as cases in which $\alpha \neq 0$ are concerned, the density effect on the oviposition rate may change from an Allee type to a *Drosophila* one if the period of incubation is suitably prolonged. This agrees qualitatively with Chapman's and Park's experimental results as cited in the introduction of this paper.

Next, keeping t_* and β fixed, the Z *vs.* N plots were computed for different values of α, and are plotted in Figure 5. The figure shows that when $\alpha = 0$, the plot is simply of the *Drosophila* type, while when $\alpha \neq 0$, the plots always possess a maximum, thus having a good resemblance to the Allee type. However, even in cases in which $\alpha \neq 0$, the optimum density points are screened below the smallest possible density if the values of α are relatively small. This indicates that for smaller values of α the density effects of the *Drosophila* type are to be observed experimentally. As noted previously, larger values of α are associated with smaller copulation tendencies, so that the appearance of density effects of the Allee type can be attributed, so far as the present theory is concerned, to a lower tendency for collision of parent adults. A similar but too qualitative in-

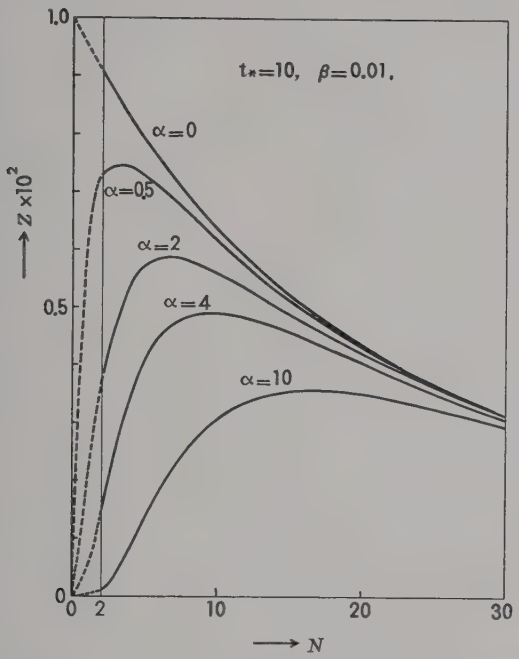

FIG. 5. Effect of the copulation tendency on the shape of the Z *vs.* N plot; for α, see equation (3) in the text.

terpretation for the cause of the density effects of the Allee type is given by Allee *et al.* in their famous book (Allee *et al.* 1950).

From these considerations it may be mentioned that both the *Drosophila* and Allee types of density effect on oviposition rate are not different qualitatively or essentially from one another but differ only quantitatively through the parameters t_* and α. As has been noted by Utida (1950), the only point to be distinguished is that some kinds of insect possess optimum density points below the smallest possible density, while others have such points at relatively high densities. Although it may be too drastic to ascribe this behavior only to the relative values of the parameters t_* and α, there is no doubt that these parameters are operating as the important factors controlling population dynamics.

ACKNOWLEDGMENT

The author wishes to express his sincere appreciation to Professor S. Utida, Entomological Laboratory, Faculty of Agriculture, Kyoto University, for interest and support given in the course of this work.

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THE ECOLOGY OF SERPENTINE SOILS*

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THE ECOLOGY OF SERPENTINE SOILS

I. INTRODUCTION

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Areas of the soil-rock systems which may be grouped together as "serpentines" occur in many parts of the world and, wherever they occur, are known for their remarkable plant life. Many authors have described the flora and vegetation of serpentine areas in Europe: Sweden (Rune 1953),[1] Norway (Bjørlikke 1938), Finland (Kotilainen 1944, Rune 1953), Helgoland (Dahl 1912, 1915), Great Britain (Hunter & Vergnano 1952), Austria (Hayek 1923, Nevole 1926, Lämmermayr 1926, 1927, 1928a, 1928b, 1934, Kretschmer 1931), Czechoslovakia (Zlatník 1928a, 1928b, Suza 1928, Novák 1928), Switzerland (Beger 1922-3, Braun-Blanquet & Jenny 1926, Zollitsch 1927, Braun-Blanquet 1951), Yugoslavia (Pančič 1859, Novák 1928), Albania (Markgraf 1925, 1932), Greece (Boydell 1921, Turrill 1929), Italy (Messeri 1936, Negodi 1941, Bargoni 1943, Pichi-Sermolli 1948), Spain (Palacios 1936), and France (LeGendre 1919). Serpentine vegetation is reported also from the Ural Mountains (Novák 1926, Sočava 1927, Iljinski 1936), Southern Rhodesia (Blackshaw 1921), Japan (Yamanaka 1951-2, 1952, Kitamura 1950, 1952a, 1952b, Kitamura *et al.* 1950, 1952, 1953), Karakelang in Indonesia (Lam 1927), New Caledonia (Däniker 1939, Birrell & Wright 1945), New Zealand (Betts 1918, Cockayne 1921: 332), Cuba (Seifriz 1940, 1943, Carabia 1945, Beard 1953), Puerto Rico (Holdridge 1945), Newfoundland (Fernald 1911), Quebec (Low 1884, Fernald 1907, Raymond 1950, Scoggan 1950, Rune 1953), British Columbia, and the United States. Apparently no information on vegetation is available from some areas of serpentine.

In the United States, scattered outcrops occur along the Appalachian chain from western Massachusetts through the largest Appalachian areas, those of Pennsylvania and Maryland (Harshberger 1903, 1904, Shreve 1910, Pennell 1910, 1913, 1930, Braun 1950: 248), south to Georgia (Radford 1948). The Pacific Coast states contain much more extensive areas of serpentine. The California formations (Mason 1946b, Kruckeberg 1951, and the following papers by Walker 1954, and Kruckeberg 1954) in the Sierra Nevada and the Central and North Coast Ranges total several thousand square miles. The major Oregon areas adjoin those of the California Coast Ranges and occupy much of the Siskiyou Mountain Range. The principal locations in Washington are about one hundred square miles in the Wenatchee Mountains in a belt lying just south of Mt. Stuart, about thirty square miles in the Twin Sisters Range southwest of Mt. Baker, and portions of the San Juan Islands.

These widely scattered serpentine areas have many features in common. In almost all cases they: (1) are sterile and unproductive either as farm lands or timber lands, (2) possess unusual floras, characterized by narrowly endemic species of great interest to the plant taxonomist and geneticist, and (3) support vegetation in striking physiognomic contrast with that on other soils. The problems of serpentine soils are thus both economically important and of special interest to biologists of several fields. The three features of

* A symposium originally presented at the meetings of the Northwest Scientific Association, Spokane, Washington, December 29, 1950, by R. H. Whittaker (presiding). Washington State College, R. B. Walker, University of Washington, and A. R. Kruckeberg, University of Washington.

[1] These citations are listed with those of the following paper by Whittaker (see p. 000). For additional European papers see Novák (1928), Pichi-Sermolli (1948), and Rune (1953).

serpentine areas above suggest three parts into which discussion of biological problems of serpentine may naturally be divided: the edaphic, concerning the soil itself and its relation to plant ecology; the autecological, dealing with the responses of plant species to serpentine and non-serpentine soils; and the synecological, considering the peculiarities of serpentine vegetation. In the three papers following, students of these three aspects of the serpentine problem in the western United States will attempt to present a synthesis of what is known concerning the ecology of serpentine soils.

THE ECOLOGY OF SERPENTINE SOILS

II. FACTORS AFFECTING PLANT GROWTH ON SERPENTINE SOILS[1]

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The distinctive vegetations of soils derived from serpentine and related rocks sharply set apart such areas from adjacent non-serpentine terrain in many regions of the world. The plant life of these serpentine areas varies greatly with location, topography, depth of soil, and other factors, but is usually sparse or stunted, and characterized by the presence of many species which seem to be restricted to the serpentine habitat. Many of the species present on adjacent non-serpentine soils fail to appear on the serpentine; others grow on the serpentine but are stunted, while only a few plants grow equally well on either type of soil.

These vegetational differences often serve to delineate the geologic discontinuities of an area even to the casual observer. An example of such differences is shown in Figure 1, a scene in Lake County, in the North Coast Ranges of California. On the left is a serpentine area (Soil W-30, Table II), on which the predominant woody species are Digger pine, *Pinus sabiniana* Dougl., chamise, *Adenostema fasciculatum* H. and A., leather oak, *Quercus durata* Jeps., musk-brush, *Ceanothus jepsonii* Greene, silk tassel bush, *Garrya congdoni* Eastwood, and Christmas berry, *Photinia arbutifolia* Lindl., and on which a sparse herbaceous flora occurs, including *Chaenactis glabriuscula* D. C., *Clarkia concinna* (F. and M.) Greene, *Eriogonum nudum* Dougl., *Eriophyllum lanatum* (Pursh) Forbes, *Gilia capitata* Dougl., *Phacelia corymbosa* Jeps., *Plantago erecta* Morris, *Streptanthus glandulosus* Hook., and *S. Breweri* Gray. On the right, lies a non-serpentine hillside (Soil W-53, Table II), on which is found an open stand of blue oak, *Quercus douglasii* H. and A., and a dense herbaceous cover which includes *Avena fatua* L., *Bromus* spp., *Brodiaea laxa* (Benth.) Wats., and numerous other species. The type of chaparral characteristic of serpentine areas covers thousands of acres in the California Coast Ranges, and can be distinguished at a glance from the oak-grass vegetation of hillsides of non-serpentine origin.

In other regions, comparable contrasts exist between serpentine and non-serpentine areas. In Oregon and Washington, slopes whose soils have been derived from serpentine or related rocks may be recognized readily by their barren, sparsely forested appearance, which contrasts with the presence of heavier forests on adjacent non-serpentine terrain. Robinson *et al.* (1935) describe the infertile and barren soils formed from serpentine rock in Maryland and Pennsylvania which support scrubby timber or poor farm crops, in contrast with the fertile soils of surrounding non-serpentine areas. The serpentine formations of Europe weather into sterile residual soils on which occur characetristic endemic species (Braun-Blanquet 1932, Novák 1928). Birrell and Wright (1945) described a serpentine soil in New Caledonia which bears a xerophyllous shrub vegetation from 3-5 feet high, a most unusual appearance in this region of high rainfall in which tropical forest is the ordinary plant cover. These examples serve to indicate that the uniqueness of serpentine floras is not a peculiarity of one region alone, but is world-wide in nature. A detailed discussion of the floristics of serpentine vegetation will be given by Whittaker (1954).

The striking differences often observed between the plant covers of serpentine and adjacent non-serpentine areas have naturally led to attempts to

[1] The material reported in this paper is largely taken from the author's dissertation for the Ph.D. degree in the Department of Botany, University of California, Berkeley. The encouragement and supervision of Professors A. R. Davis, H. L. Mason, and P. R. Stout, and the generous assistance of Dr. J. Vlamis are gratefully acknowledged.

FIG. 1. Barren, brush-covered serpentine hills (left) and blue-oak covered non-serpentine hillside (right) separated by a meadow of mixed rock origin. Lake County, California.

explain these phenomena in terms of the physical or chemical properties of the soil, or of the physiological characteristics of the plants. Frequently it has been supposed that plants restricted to, or endemic on, serpentine "require" some features of serpentine soil for proper growth, but the validity of this hypothesis can readily be attacked on the basis that a considerable number of these plants have been cultivated successfully in non-serpentine soils and even in culture solutions. Another common suggestion is that the endemic species grow well on the rather barren serpentine sites where competition is not severe, and are unable to survive on other soils where competition is more rigorous; but this is a suggestion that has been difficult to test experimentally. It is apparent that both the endemic and non-endemic species which grow successfully on these soils possess a "tolerance" for the serpentine habitat which is lacking in the greater number of plants which will not grow readily on this medium, and further that the non-endemic species possess some characteristic which is lacking in the endemic species. The problems of the possible restriction of endemic species to serpentine through competition and the differences which may exist between endemic and non-endemic species will be discussed in the paper by Kruckeberg (1954) which follows. The balance of this paper will be devoted first to an outline of the general attributes of serpentine rocks and soils, followed by discussions of the various hypotheses which have been advanced to explain the tolerance or intolerance of plants for serpentine soil.

Chemical Properties of Serpentine Rocks and Soils

Serpentine rock is essentially a magnesium iron silicate, formed by metamorphosis from peridotite. Although peridotite is often predominantly olivine, $(Mg, Fe)_2SiO_4$, varying amounts of pyroxenes and amphiboles are also present, so some Ca, Al, Na, and Ti are included. Also, in many instances chromite, $FeCr_2O_4$, and garnierite, (Ni, Mg) $SiO_3 \cdot n\ H_2O$, occur in appreciable proportions. These variations in the composition of the rock are reflected in the color, which may range from shiny green to bluish or almost black. Soils formed from the rock are usually reddish, brown, or gray in color at the surface, often changing to yellowish or greenish in the lower layers. Soils formed from unserpentinized peridotite and peridotite-

serpentine mixtures have similar physical and chemical properties, so it will be convenient to refer to all these similar forms under the general term "serpentine soils" in this discussion. Since there is a wide range in the composition of the parent rocks, it is to be expected that the compositions of the resultant soils should vary considerably, especially in the secondary constituents such as calcium, potassium, and the heavy metals. Even small variation in these elements may have marked effects, however, on the ability of the soils to support plant growth.

While the total composition of the parent rocks is only one of the factors involved in the formation of soil, it is of considerable interest to examine analyses of some of these basic igneous rocks, and of soils of this origin (Table I). The contents of the major constituents, Si, Mg, and Fe, are in the same range in the rocks; aluminum is low in all cases; and values for all the other elements are under one per cent. Although the contents of calcium and the heavy metals are small, they will be seen to play important roles in some of the hypotheses which attempt to explain the intolerance of plants for serpentine soils. Magnesium content is reduced by weathering, and is seen to be much lower in the soils than in the rocks; it was noted by Robinson *et al.* (1935) that in most cases magnesium is lower in the surface soil than in the deeper soil layers. Loss of this element is striking in tropical soils such as the one from New Caledonia, in which the accumulation of iron is also particularly noticeable. Chromium is also especially high in the tropical soils, either because of its abundance in the parent rock or an accumulation similar to that of iron.

It is questionable whether the total analyses quoted above give reliable indications of the amounts of the various ions which are available for plant absorption. Important among the types of analyses which are intended to measure the levels of ions available to plants is the determination of the exchangeable cations by means of the ammonium acetate extraction method. The exchangeable cation values, as well as H-ion concentrations, for a number of serpentine and non-serpentine soils are given in Table II. The problems of the forms of chromium and nickel which exist in the soil and which may be absorbed by plants have been studied very little, but values for the exchangeable form of these ions are included in the table where available. Since the percentage of calcium present among the exchangeable cations is considered to be of particular importance in connection with soil fertility, this is also included in Table II. The table shows that magnesium much exceeds calcium except in the tropical soil from New Caledonia. The data also show that there is a considerable range of calcium levels among the serpentine soils, even though all are low in this element. It will be shown later how such differences may greatly influence the degree of infertility of a particular soil.

TABLE I. *Total chemical analyses of certain rocks and soils*

	Fresh serpentine rock, Cherry Hill, Maryland (Robinson *et al.* 1935) Per cent	Peridotite (90% olivine)†, Whatcom County, Washington (Pfeiffer 1945) Per cent	Serpentine soil material, Mt. Tamalpais, California (Robinson *et al.* 1935) Per cent	Serpentine surface soil, Dublin, Maryland No. 4722 (Robinson *et al.* 1935) Per cent	Serpentine soil, 5-15 in., New Caledonia (Birrell & Wright 1945) Per cent
SiO_2	37.98	43.7	40.28	66.30	3.95
TiO_2	0.10	**	0.12	0.83	—
Al_2O_3	0.78	1.5	2.36	7.17	—
$Al_2O_3+TiO_2$	—	—	—	—	4.87
Fe_2O_3	12.45	—	9.31	6.44	71.9
FeO	—	7.3			—
MnO	0.1o	**	0.13	0.09	**
Cr_2O_3	0.44	**	0.29	0.17	3.05
NiO	**	Trace	0.25	0.003	0.16
CaO	Trace	0.3	Trace	0.20	0.05
MgO	37 68	46.6	36.42	12.96	0.06
K_2O	0.06	**	Trace	0.66	—
Na_2O	0.01	**	0.02	0.53	—
P_2O_5	0.03	**	0.02	0.03	—
SO_3	0.52	**	0.08	0.13	—
Alkalis and undetermined	—	—	—	—	0.84
Ignition loss	10.35	+2.5	12.25	5.55	15.12

†From same area as soil W-207 (*cf.* Table II).
**Not determined.
— Included in another category.

Physical Characteristics of Serpentine Soils

Peridotite and serpentine formations are usually intrusions of great depth and often of ancient geologic origin; thus it might be anticipated that the soils would be deep, and such is the case in many of the Conowingo soils of Maryland, and in tropical soils which have been described (Robinson *et al.* 1935, Birrell and Wright 1945). On the other hand, many serpentine sites are in rolling or mountainous terrain, and the soils in such locations are usually shallow, presumably because the steepness of the slopes and the sparseness of the vegetation encourage continual erosion. In many cases, these soils are made up largely of relatively unweathered rock particles, and may be called lithosols; in many other instances, the shallow soils contain considerable clay and organic material and might better be called azonal soils of a relatively stable nature. Robinson *et al.* (1935) believe that some serpentine rocks are too low in alumina to form sufficient clay for the establishment of a normal soil covering, regardless of the topography. This hypothesis concerning insufficient clay formation may explain the existence of

TABLE II. *Exchangeable cations in soils*

Soil No.	Location and description	Parent material	pH	Exchangeable cations milliequivalents/100 gm soil						NH_4 adsorp. capacity m. e./100 gm	% Ca
				Ca	Mg	K	Na	Ni	Cr		
(B & W)*.....	New Caledonia	Serpentine									
	0-5 in. layer		5.8	0.6	0.8	**	**	0.12	0.026	9.8	6.1
	5-15 in. layer		5.4	0.6	0.3	**	**	**	**	3.5	17
REB† 4722...	Dublin, Maryland	Serpentine	5.85	0.16	4.09	0.06	0.13	0.012	0.006	**	**
W-30‡.....	Lake Co., Calif.	Serpentine	6.80	2.12	12.1	0.11	0.05	0.026	0.001	14.2	14.9
W-37.....	Lake Co., Calif.	Serpentine	6.60	2.33	19.7	0.13	0.04	**	**	22.3	10.4
W-52.....	Marin Co., Calif.	Serpentine	6.35	3.20	11.2	0.37	0.13	0.003	**	17.0	18.8
W-53.....	Chelan Co., Wash.	Serpentine	6.62	2.03	5.95	0.20	**	**	**	8.66	23.4
W-207.....	Whatcom Co., Wash.	Peridotite	6.21	1.07	9.16	**	**	**	**	13.1	8.2
W-38.....	Solano Co., Calif.	Sandstone	7.20	11.1	3.2	0.23	0.09	**	**	13.1	84.7
W-53.....	Lake Co., Calif.	Sandstone	6.75	23.4	11.2	1.42	0.14	0.005	nil	30.6	76.4

*Data from Birrell and Wright (1945). †Data from Robinson, Edgington, and Byers (1935).
‡The prefix *W* indicates data of the author. **Not determined.

only a thin soil mantle on many rather level areas. The textures of the soils vary from heavy clays to light loams, with a friable, gravelly loam being the most common type in western United States. From a series of detailed physical analyses, Robinson *et al.* (1935) concluded that serpentine soils possess no physical characteristic which would render them particularly unfavorable for plant growth, although in some cases the clay contents of the subsoils were high enough to impede drainage.

Undesirable physical characteristics, such as shallowness of the soil mantle, gravelly texture, low clay content, and steepness of topography which encourages erosion, have important effects on the vegetation of serpentine areas, since they result in reduced moisture and nutrient levels. On moister serpentine sites, such as north slopes, the plant cover is more abundant, and often includes additional species which are absent in drier situations. This presumably indicates, at least in western United States, that plants which are widespread on serpentine soils possess drought resistance as well as tolerance for serpentine soils. The various physical factors may have effects in connection with soils of diverse parent materials, however, so the peculiarities of serpentine soils do not appear to be explicable on the basis of physical characteristics.

HYPOTHESES ADVANCED TO EXPLAIN TOLERANCE AND INTOLERANCE FOR SERPENTINE SOILS

A number of hypotheses have been advanced which attempt to explain the peculiarities of serpentine soils on the basis of soil chemistry. The development of different viewpoints on the subject probably can be attributed to the fact that the soils studied came from different climatic regions and to the probability that two or more of the proposed factors may operate simultaneously in many of the soils. A discussion of each of the major hypotheses follows in the succeeding paragraphs. Most of these hypotheses have stemmed from the studies by agriculturalists of the infertility of these soils for crop plant production. From the agricultural viewpoint, *serpentine infertility* is equivalent to *serpentine intolerance* by crop plants, so these two terms will be used interchangeably below.

(1) Low levels of major nutrient elements

Gordon and Lipman (1926) observed low levels of nitrate and phosphate ions in the soil extracts which they studied, showing that these ions limited the growth of barley. Later, Vlamis (1949) demonstrated that lettuce and barley responded markedly to nitrogen and phosphate additions to a serpentine soil. The nature of such response in both an agricultural species, the tomato, *Lycopersicon esculentum* Mill., and a non-endemic but serpentine-tolerant species, the wall-flower, *Erysimum capitatum* (Dougl.) Greene, is shown by the results of greenhouse pot culture experiments in Table III (Walker 1948a). The soil used was obviously very deficient in nitrogen and moderately deficient in phosphorus, although it is recognized that under natural conditions in which water or other factors may be limiting growth, such deficiencies would be less severe. It is also a common observation that many types of soils, regardless of origin, are deficient in these elements. In a recent experiment, a serpentine soil from Chelan County, Washington, showed a severe deficiency of sulfur when tested with tomato plants in pot cultures. No doubt deficiencies of major nutrient elements are common in serpentine soils, but there is little evidence that any such deficiency can serve as a general explanation of poor plant growth on these soils, because in agricultural practice, heavy applications of nitrogen,

TABLE III. *Effects of nitrogen, phosphorus, and potassium additions to a California serpentine soil (W-30) on the yields of tomato and wall-flower, Erysimum capitatum*

Fertilizer addition	Weight of shoot (dry gm)	Per cent of NPK yield
	Tomato	
None	0.61	12
NPK	5.06	100
	Erysimum capitatum	
None	0.24	7
NPK	3.42	100
PK	0.27	8
NK	1.82	53
NP	2.98	87

phosphorus, potassium, and sulfur have failed to correct their infertility.

(2) Alkalinity

Gordon and Lipman (1926) suggested that the alkaline reaction of serpentine soils contributes to their infertility. Whereas the Californian soils with which they worked are alkaline, this is not true for the majority of serpentine soils, and it is also known that many somewhat alkaline soils of diverse origins are quite fertile. It is apparent that alkalinity cannot serve, in any case, as a general explanation for serpentine infertility.

(3) Low available molybdenum

It has been found that a number of the Californian serpentine soils are deficient in available molybdenum (Walker 1948b, Johnson, Pearson, and Stout 1952). This can be demonstrated by growing agricultural species such as tomato and lettuce in pot cultures with heavy nitrogen and phosphate fertilization. As yet, no investigation has been made to determine whether or not this low molybdenum level is characteristic of serpentine soils in general, nor are any data available to indicate whether native plants may suffer from a deficiency of this element. Such deficiency in the field seems somewhat unlikely in view of the slow growth rates of the plants, so it appears reasonable to state at present that molybdenum deficiency may contribute to the infertility of some serpentine soils, but is probably not the dominant factor in any case.

(4) Toxicity of chromium, nickel, or other heavy metals

It has been proposed that the presence of toxic concentrations of heavy metals such as chromium and nickel may be responsible for the unfavorable nature of serpentine soils for plant growth (Robinson *et al.* 1935, Birrell and Wright 1945). Unquestionably, the chromium and nickel contents are generally higher in serpentine soils than in those of other origins, and appreciable amounts of these metals may be absorbed by plants. The amounts absorbed may be as high as 86 parts per million Ni and 4.5 parts per million Cr in the dry leaf material of *Pancheria glabrosa* growing on a tropical soil with pH of 5.8 in the surface horizon (Birrell and Wright 1945). These values are considerably higher than the levels found in either field- or greenhouse-grown tissue from several neutral serpentine soils of western United States (Table IV). Little is known about the factors affecting the absorption of nickel and chromium from soils, but it is probable that the pH, the nature of the primary and secondary minerals, the concentrations of anions such as phosphate, and perhaps other soil characteristics have considerable influence on the uptake of the heavy metals. The importance of pH in nickel availability was stressed by Hunter and Vergnano (1952), who studied a glacial area in Scotland in which the parent material is largely serpentine rock. Oats growing on soils in this area accumulated 16 to 134 parts per million Ni in the expanded leaves,

TABLE IV. *Nickel and chromium analyses of leaf tissue collected on serpentine soils*

Species	Location	Reference*	Parts per million in dry leaf tissue	
			Ni	Cr
Blackjack oak	Dublin, Maryland	Robinson *et al.* (1935)	4	4
Red oak	Dublin, Maryland	Robinson *et al.* (1935)	5	3
Pancheria glabrosa	New Caledonia	Birrell and Wright (1945)	86.3	4.5
Araucaria mulleri	New Caledonia	Birrell and Wright (1945)	19.3	12.6
Garrya congdoni	Lake County, California		12	nil
Quercus durata	Lake County, California		8.2	0.30
Arctostaphylos sp.	Lake County, California		10	0.43
Marglobe tomato	Grown in pots on soil W-30 from Lake County, Calif.		29	1.5
Pseudotsuga taxifolia	Chelan County, Washington (Soil W-85)		3.7	0.32
Marglobe tomato	Grown in pots on soil W-85 from Chelan County, Washington		5.8	1.6

*Analyses not otherwise credited are those of the author.

the larger amounts being absorbed from the more acid soils and the smaller amounts from the less acid fields. Concentrations of 30-40 parts per million in the leaves of young plants caused moderate toxicity symptoms, and higher concentrations caused more severe chlorosis and necrosis, present in longitudinal stripes.

Toxicity symptoms were noted by the writer in tomato and sunflower (*Helianthus*) plants grown in culture solutions if the concentrations of chromium or nickel in the solutions were sufficiently high to reduce plant growth appreciably. However, tomato and sunflower were grown on several serpentine soils from western United States (in which the calcium was raised to a favorable level) with excellent growth and with absence of toxicity symptoms. This may be, of course, merely further evidence that plants absorb less nickel from these nearly neutral soils than from more acid ones. Another aspect of toxicity which needs investigation with respect to serpentine soils is the fact that additions of molybdenum may alleviate toxicities caused by excessive nickel, manganese, or other cations in culture solutions (Milliken 1948).

As yet, there is insufficient evidence at hand to evaluate the toxicity hypothesis critically. Large amounts of chromium and nickel may be absorbed from some acid serpentine soils, but much less is available to plants from neutral soils. While this toxicity factor is of much importance in specific areas, it seems unlikely that it is alone responsible for the world-wide peculiarity of the serpentine habitat.

(5) Status of calcium and magnesium in the soil

The predominance of magnesium over calcium in the ferro-magnesian rocks and soils was advanced by Loew and May (1901) as the reason for poor growth on serpentine soils. They determined the calcium and magnesium contents of many soils by acid extraction or by total analysis and related these values to the productivity of the soils, concluding that the Ca : Mg ratio in the soil should equal at least one for good plant growth. Recently Vlamis and Jenny (1948) have used low calcium saturation of the soil colloids as a modern replacement for the old ratio hypothesis, attributing little importance to the magnesium except that it makes calcium less available. The amounts of adsorbed calcium and magnesium in some serpentine and non-serpentine soils are listed in Table II. The quantity of calcium is low in every case, but there is considerable difference in the percentage saturation with this ion. Magnesium is the predominant cation in the neutral or moderately acid serpentine soils of the temperate zone, while it may be almost entirely replaced by hydrogen in the highly weathered tropical ones.

Vlamis (1949) demonstrated the relationship between calcium saturation of the soil and the yield of barley and lettuce, obtaining yields which were very low at 10% saturation, increased sharply up to 20-25%, and leveled off at saturations above 25%. The author has performed a series of experiments involving both agricultural and native species which lend considerable support to the calcium saturation viewpoint (Walker 1948a). In the technique used, individual lots of the field serpentine soil were leached with chloride solutions varying in calcium and magnesium as desired. After leaching, excess salt was washed out with water; the soils were dried, fertilized with NPK, and used for greenhouse pot cultures. In this manner, soil lots were prepared in which calcium varied from 5% to 80% of the total exchangeable cations, with magnesium varying in a complementary manner from 94% to 19%, and potassium remaining in all cases at about 1%. The results of representative experiments in which tomato, *Lycopersicon esculentum* Mill., variety Marglobe, was compared with an endemic species of crucifer, the jewel flower, *Streptanthus glandulosus* var. *pulchellus* (Greene) Jeps., are given in Table V.

These data indicate that the growth of tomato is much restricted at the calcium level of the field soil, is reduced to nil as the saturation of 5.6% is reached, but increases strikingly at the calcium levels above that of the field soil. In contrast, the yields of the *Streptanthus* plants were little changed by the calcium level. This indicates that the endemic species is more tolerant of the low-

TABLE V. *Yields and leaf composition of Marglobe tomato and Streptanthus grown on lots of serpentine soil (W-30) with varying Ca saturation*

Per cent Ca saturation of soil	Average yield of shoot, dry grams	Per cent of yield on field soil	Leaf-tissue analyses, milliequivalents per 100 dry grams		
			Ca	Mg	K
	Marglobe tomato				
5.6	0.03	1.1	**	**	**
8.3	0.09	3.2	27.7	442	28.5
12.5	2.16	82	30.8	246	59.9
13.5*	2.63	100	35.5	233	50.2
25	7.74	294	38.2	117	29.9
34	7.52	286	54.7	99.8	38.5
	Streptanthus glandulosus var. *pulchellus*				
5.6	3.73	75	21.8	222	56.8
8.3	3.59	73	26.8	166	58.3
12.5	3.68	74	54.6	120	58.6
13.5*	4.95	100	52.1	121	42.7
25	4.42	89	85.7	84.2	51.2

*Unaltered field soil.
**Plants died before end of growth period.

calcium medium than tomato, which seems to offer a physiological explanation for serpentine tolerance. Similar experiments performed on other agricultural species (lettuce, *Lactuca sativa* L., var. Romaine, and sunflower, *Helianthus annuus* L., var. Russian Mammoth), and two other native species (serpentine-collected races of *Helianthus bolanderi* Gray, subsp. *exilis* (Gray) Heiser, and *Streptanthus glandulosus* Hook.) have given results of a similar nature. Native species which do not invade serpentine areas react to low calcium levels as do the agricultural species (Kruckeberg 1954).

Reasons for the differences in responses of various plants to soils of low calcium saturation are not apparent. One indication may lie in the results of calcium and magnesium analyses of the leaf tissue. In Table V it is seen that the *Streptanthus* absorbed somewhat more calcium than the tomato at comparable soil calcium levels, but the most noticeable difference is that the magnesium absorption of the tomato greatly exceeded that of *Streptanthus* at the very low calcium saturations. This excessive magnesium in the tissues could in some way hamper the normal utilization of the calcium which is present, perhaps simply by ion competition at membranes or sites of absorption, so that the ratio of calcium to magnesium is apparently more important than the absolute amount of calcium. In lettuce and tomato, a Ca : Mg ratio in the tissue of less than 0.20 is accompanied by reduced yield and at least incipient calcium deficiency, while ratios of less than 0.15 are associated with severe calcium deficiency symptoms and great reductions in yield.

The results reported above lend confirmation to the proposal of previous workers (Loew and May 1901, Vlamis and Jenny 1948) that the basic cause of serpentine infertility is the low calcium level, and the writer is of the opinion that in the larger picture of serpentine tolerance and intolerance this is likewise the principal factor. The role played by the other adsorbed cations in relation to calcium is not clear, however, and probably varies with different soils. The data given above indicate that ability to exclude magnesium may be a characteristic of the tolerant species, but in some tropical serpentine soils magnesium has been replaced to a large extent by hydrogen, and, in such cases, unbalance between calcium and magnesium can be of no importance. Vlamis and Jenny (1948) noted that large amounts of adsorbed potassium or strontium had effects similar to magnesium in inducing calcium deficiency. Although the relationships of adsorbed hydrogen to the other cations and to the general problems of soil infertility have received much attention (Heslep 1951), there is a lack of agreement concerning effects of hydrogen. It is thus difficult to compare the usual high-magnesium serpentine soils with those in which most of the magnesium has been replaced with hydrogen. It is evident, however, that in the latter group, calcium saturation is extremely low and probably of considerable importance even if a factor such as heavy metal toxicity should predominate in controlling plant growth.

Discussion

Low levels of adsorbed calcium have been shown to limit the growth of serpentine-intolerant species, as represented by a number of common crop plants, but serpentine endemic species are tolerant of calcium levels even lower than are usually found in natural serpentine soils. There is no doubt that only those plants which possess the ability to thrive on soils of low calcium status can long persist in serpentine areas, while plants lacking this ability will be excluded from them.

The effects of nickel and chromium depend upon their availability in the soil, the amounts absorbed by plants, and the sensitivity of individual species to these metals. The amounts absorbed from some soils by the native species appear to be sufficiently high that more sensitive species might be expected to be adversely affected, but this has not been confirmed by experimentation. On other soils, even though the total nickel and chromium contents are known to be high, absorption by sensitive crop plants is insufficient to induce toxicity. It is apparent that considerable experimentation involving serpentine soils from different regions will be necessary before aspects of toxicity can be evaluated fully.

It is concluded that the basic reason for the intolerance exhibited by most plants for serpentine soils is the low calcium level. In special cases, heavy-metal toxicity may be more influential than the calcium saturation, or at least serve as an additional major factor limiting plant growth. The possible effects of low available molybdenum and high magnesium concentrations have yet to be fully evaluated, but the influence of magnesium in accentuating calcium deficiencies must be of importance in most serpentine soils. Often factors not unique in serpentine sites, such as limited water retention and low levels of various major nutrients, contribute to making the serpentine environment unsuitable for many species. Plants which grow well on serpentine soils must therefore first be tolerant of low calcium levels and, in addition, be tolerant of one or more of the following: high concentrations of chromium and nickel, high magnesium, low levels of major nutrients, low

available molybdenum, and the drought and other undesirable aspects of shallow, stony soils.

Summary

1. In an attempt to elucidate the factors involved in the tolerance of some plants for serpentine soils and the intolerance of others for this unusual growth medium, a description has been made of the physical and chemical properties of these soils, followed by an examination of the various hypotheses which have been advanced to explain the peculiarities of the soils with respect to plant growth. They differ from other soils in these principal characteristics: low contents of total and adsorbed calcium, high magnesium content, and high contents of chromium and nickel.

2. Serpentine areas usually support a stunted type of vegetation, unique in its species composition. Such an area located in California is described.

3. It is well-established that these soils are infertile for the growth of most plants, yet are tolerated by certain others. The following hypotheses, which have been advanced to explain tolerance and intolerance of serpentine soils, are examined: various physical factors, low levels of major nutrient elements (especially nitrogen and phosphorus), alkalinity, low available molybdenum, toxicity of nickel or chromium, and the status of calcium and magnesium in the soil. While all of these have effects under certain circumstances, experimental evidence favors the view that low calcium level is the basic cause of the peculiarity of serpentine soils, with the other factors of secondary importance.

4. It is concluded that plants which grow well on serpentine areas must first be tolerant of low calcium levels and, in addition, must be tolerant of one or more of the following in special situations: high concentrations of nickel and chromium, high magnesium, low levels of major nutrients, low available molybdenum, and unfavorable physical aspects of shallow soils.

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THE ECOLOGY OF SERPENTINE SOILS

III. PLANT SPECIES IN RELATION TO SERPENTINE SOILS

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The North Bay counties (Napa, Lake, Marin, and Sonoma) of central California have afforded an ideal locale for study of the vegetational discontinuities associated with serpentine outcrops. Here, large areas of serpentine rocks are exposed; and one is impressed at once by the sharp contrasts among vegetation types. Walker (1954) has described in detail the distinct differences in vegetation that exist between the two soil phases of this mosaic of serpentine and non-serpentine formations. The gross differences in aspect between the two types of vegetation are particularized when a tabulation of species is made. The vegetation of non-serpentine areas consist mostly of species common to similar sites throughout central California whereas serpentine outcrops support a flora rich in endemic species. Such sclerophyllous shrubs as *Quercus durata* Jeps., *Ceanothus jepsoni* Greene, *Garrya congdoni* Eastwood, and even the small tree, *Cupressus sargentii* Jeps., are unmistakable "indicator" species because of their typical restriction to and numerical dominance on serpentine soils. Although not endemic to serpentine, *Adenostoma fasciculatum* H. & A. and *Photinia arbutifolia* Lindl. are likewise characteristic dominants in this vegetation pattern.

It is not these dominant woody species, however, which have made these serpentine areas celebrated as a source of rare and endemic plants. The transient spring flora of these dry serpentine hills still continues to be a source of "new or otherwise noteworthy" additions to the California flora. The list of diminutive annuals and herbaceous perennials that merit the serpentine endemic status is increased every year. From all accounts (Morrison 1938, 1941, Stebbins 1942, Mason 1946, Hoffman 1952), genera of the annual lifeform are by far the richest source of variation throughout the serpentine mosaic of central California. One of the genera most characteristic of the serpentine areas is *Streptanthus,* which will serve as an example of some of the genetic problems of serpentine endemism.

The distributional responses of different plant species to serpentine soils raise three groups of problems: (1) Why are so many species excluded from serpentine soils?, (2) Why are other species, which occur with them off serpentine, able to grow successfully on serpentine?, (3) Why is a third group of species restricted to serpentine soils? In this paper these three questions will be examined further, seeking genetic and ecologic, as well as edaphic, answers.

TOLERANCE TO SERPENTINE SOILS

From the careful work of Vlamis & Jenny (1948), Vlamis (1949), and Walker (1948, 1954), we may state a working hypothesis on serpentine tolerance: A major criterion for serpentine tolerance must be the capacity of serpentine plants to grow on soils of *low calcium* levels. It has been shown by these authors that crop plants, which grow poorly in serpentine soils, are unable to absorb sufficient calcium from them. In addition, Walker (1948) proposed that serpentine endemics appear to be characterized by their ability to obtain sufficient calcium, even at the low concentrations characteristic of serpentine soils. Some native species occur both on and off serpentine, however, and studies of these may further clarify the problem. We might expect to find, within species of this latter type, some populations adapted to serpentine and others not so adapted. The demonstration of such serpentine and non-serpentine races, if they do exist, would provide some basis for a genetic interpretation of serpentine endemism. These species which occur both on and off serpentine may be called *bodenvag* plants (Unger 1836) in contrast to *bodenstet* species which are restricted by a requirement for a specific chemical substance in the soil. The use of serpentine and non-serpentine populations of *bodenvag* species may be especially effective in the study of serpentine adaptation, since the populations being compared should be closely similar in every respect except that with which we are most concerned—adaptation to serpentine.

Seeds of a number of *bodenvag* species were collected from both serpentine and non-serpentine sites. These paired populations of the same species were then grown on serpentine soils adjusted to different levels of exchangeable calcium. Invariably, the serpentine populations were much more tolerant of low calcium levels (less than 25% exchangeable Ca) than the populations from other soils. Some of the most striking results were ob-

tained with two strains of the *Phacelia californica* Cham.—*P. imbricata* Jeps. complex. The non-serpentine strain was from Los Alamos Creek, Sonoma County, where it grows on soil derived from basalt; the serpentine strain came from the rather extensive serpentine outcrop on Tiburon Peninsula, Marin County. Seeds of these two strains were sown on triplicated 1600-gram aliquots of serpentine soil prepared in the following manner: The series represented by pot "A" in Figure 1 was treated with gypsum ($Ca_2SO_4.2H_2O$) in the amount equivalent to 2 tons to the acre and pot "B" in amount equivalent to 4 tons to the acre, while "C" is unaltered serpentine soil and "D" the serpentine soil plus a nitrogen-phosphorus-potassium treatment ($N_3P_4K_2$). The photographs of Figure 1 show the rather clear-cut differences in growth response with these soil treatments. In line with Walker's hypothesis of tolerance to low calcium levels, it is seen that only the serpentine strain grew at the low calcium level of the field soil, whereas the non-serpentine strain required a significant calcium amendment before its growth became comparable to the serpentine form. The results of the NPK treatment shed additional light on the specificity of the effect of calcium on the growth of the two strains. Only the serpentine strain showed good growth on the fertilized serpentine soil. The non-serpentine strain grew no better on this soil than on the unaltered serpentine soil. Thus it is seen that an NPK amendment did not ameliorate the poor growth of the non-serpentine strain on a soil of low calcium level.

FIG. 1. Reaction of serpentine and non-serpentine strains of *Phacelia californica* to unaltered and reconstituted serpentine soil. Pot A: 2 tons/ acre $Ca_2SO_4.H_2O$; pot B: 4 tons/ acre $Ca_2SO_4.H_2O$; pot C: unaltered serpentine; pot D: serpentine plus $N_3P_4K_2$. Plants of serpentine and non-serpentine strains appear on right and left halves of pots, respectively.

The results of tissue analyses further substantiate the suggestion of Walker that serpentine species may absorb calcium in preference to other cations, notably magnesium. The most significant feature of the graph in Figure 2 is the difference between the two strains in amounts of calcium absorbed. Even though both strains showed increase in calcium absorption as calcium level in the soil was increased, there was a decided difference in the absolute amounts absorbed by each strain. At each of the three soil-calcium levels, the serpentine race had absorbed greater amounts of calcium *and* had absorbed less magnesium than had the non-serpentine race.

To complete the picture of the calcium effect, results of additional related experiments may be summarized:

(1) Several native *bodenvag* species were grown on a series of serpentine soils adjusted to levels of exchangeable calcium ranging from 3% to 80%. For the non-serpentine strains, the minimum calcium level for normal growth was 25% of the total exchange capacity of the soil. In sharp contrast, the serpentine strains showed vigorous growth at 13% and at least fair growth at 6%, the latter calcium level being well below that of unaltered serpentine soil.

(2) A fertile soil of the Yolo series was reconstituted so as to simulate a serpentine soil in low calcium and high magnesium levels. The growth of serpentine and non-serpentine strains of *Phacelia* on this "serpentine" Yolo soil was compared with that on an unaltered (control) Yolo soil. As might be expected, the low-calcium Yolo replica-

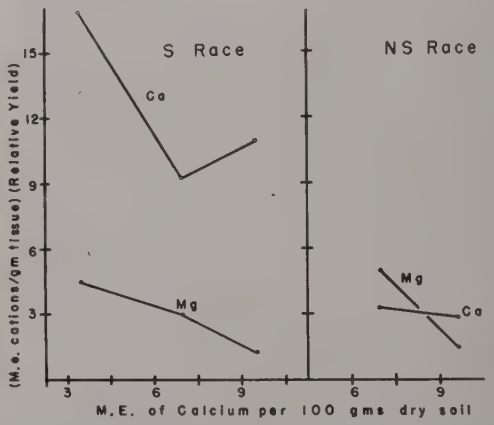

FIG. 2. Comparisons between serpentine (S) and non-serpentine (NS) strains of *Phacelia californica*. Total cation absorption (m.e. cations/gm tissue × relative yield) plotted against soil calcium level.

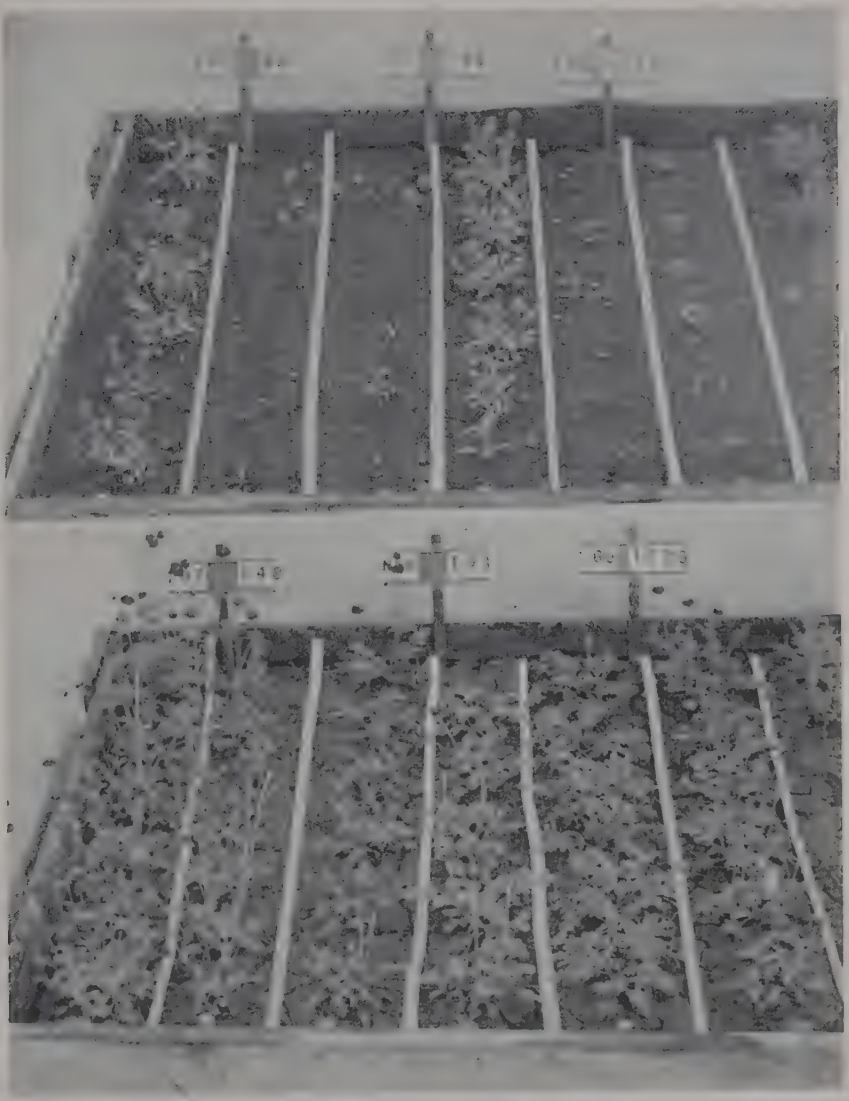

FIG. 3. Response of two serpentine and four non-serpentine strains of *Salvia columbariae* to serpentine soil (above) and non-serpentine soil (below). The serpentine strains are S-148 and S-167.

tions gave the same all-or-none picture that was so characteristic for the two *Phacelia* strains grown on unaltered serpentine soil. The non-serpentine strain was unable to grow in the "serpentine" Yolo soil, presumably because of the same adverse low calcium level as in the unaltered serpentine soil.

(3) Differences in response appeared among different *bodenvag* species. Of 21 species of several plant families tested, 12 showed definite differentiation into serpentine and non-serpentine races. Most of the annual and perennial herbs other than grasses showed the differentiation into races, but none of the grass species studied did. Several examples of the rather definitive responses of races of *bodenvag* species to serpentine are cited elsewhere (Kruckeberg 1951). The clear-cut ecotypic response of biotypes to serpentine soil is typified in the example of the annual sage, *Salvia columbariae* Benth. (Fig. 3). In contrast, the herbaceous perennial, *Achillea borealis californica* (Poll.) Keck, gave a mixed response (Kruckeberg 1951). Some non-serpentine strains of *Achillea* were quite uniform in their intolerance

of serpentine, while others were variable in this respect. As yet, the uniform tolerance of a *non-serpentine* strain (a maritime form) to serpentine soil is unexplained.

(4) Results were obtained which point to differences in low-calcium tolerance even among serpentine endemics. Certain *Streptanthus* species (subsection *Hesperides*) grew quite well in a 3% calcium soil, while others (subsection *Pulchelli*) made a much poorer showing at this extremely low calcium level. These results seem to be correlated with field observations of the distribution on serpentine outcrops of these two groups of endemic Streptanthi. The former group (better adapted to the 3% level) is more frequently found on the barren patches of "raw" serpentine and on loose, fine talus. The other group (less tolerant of the 3% level) occurs predominantly where some development of the serpentine soil has taken place.

The experimental results seem in agreement with those of Walker. The importance of factors other than calcium-level for some plants cannot be excluded, but there is good reason to stress the degree of calcium saturation of the soil as of major significance in the serpentine problem. It appears probable that an important requirement for existence of serpentine endemics on serpentine soil is their capacity to obtain calcium at low levels. It may also be held that those species growing both on and off serpentine are able to do so because either their whole populations or, more frequently, their specially adapted serpentine populations possess that same adaptation to low calcium levels. The plants growing on serpentine may, in addition, be adapted to the low levels of other nutrients, to the openness and strong exposure to evaporation in the serpentine communities, and to other factors.

That such is the case is suggested by the phemomenon of "serpentinomorphism" Many serpentine populations show at least slight morphological distinction from non-serpentine populations of the same species, and some are distinctive enough to have been named as varieties. Often the serpentine populations are of reduced stature, with denser branches and smaller, thicker, more pubescent leaves than the non-serpentine population. These characteristics of serpentine plants are discussed by Pichi-Sermolli (1948) and Rune (1953). Pichi-Sermolli recognizes six tendencies: reduction in size of leaves and other organs, shrubbiness of growth, stunting or dwarfing, greater development of the root system, increased glaucousness, and reduced pubescence (there are contrary indications of increased pubescence in some species; consistency among different species need not always be expected). Most of these differences, both in serpentine species compared with congeners and in serpentine populations of *bodenvag* species, are those to be expected of plants growing in dry and open situations. It thus seems likely that serpentine plants are physiologically adapted to the open characteristics of serpentine communities as well as to the special soil conditions, and that the physiological adaptations of serpentine plants may have some degree of morphological expression.

Genetic Aspects of Serpentine Adaptation

The foregoing results, together with field observations, may provide some basis for considering genetic and evolutionary aspects of the serpentine problem. One of the characteristic genera of serpentine plants in California, *Streptanthus,* is especially instructive in this respect (Kruckeberg 1951). All of the dozen or more species of the section *Euclisia* of this genus are serpentine plants, occurring here and there in northern California, the total range of a species being in some cases only a few square miles of serpentine. Some of these species are quite strictly confined to serpentine, others occur predominantly on serpentine but also maintain substantial populations on other soil materials. Still other species of *Streptanthus* have not been observed on serpentine, or occur predominantly on other rocks but maintain populations on serpentine.

It was, in part, some of these annual species endemic to serpentine outcrops that led Stebbins (1942) to seek a genetic explanation of endemism. Stebbins proposed that there are two types of endemics. The "depleted" species is an old (but not necessarily senescent) species which has acquired endemic status through the loss of most of its biotypes which formerly allowed the species to exploit a greater variety of habitats. Thus, by "biotype depletion," the species has been pared down to but one or a few biotypes specifically adapted to serpentine or some other local or specialized habitat. The other type of endemic, the "insular" species (which may occur as well on a continent as on an island) could have originated from a few isolated individuals pre-adapted to a specific habitat situation. Such a species, *ab initio,* is an endemic. The "depleted" and "insular" species are suggestive of the more familiar concepts of paleo- and neoendemic species, but may have little to do with age of the species.

Both types of species origin may be postulated for the serpentine endemics in *Streptanthus.* It is probable, moreover, that we can observe depletion in progress in some species. *Streptanthus glandulosus* Hook. is the most wide-spread serpentine species of the genus in California. It occurs

mainly on serpentines from San Luis Obispo County north to Del Norte County, but occasional non-serpentine localities for the species are also encountered. *Streptanthus glandulosus* was submitted to the same experimental procedures as other *bodenvag* species, with seed of both serpentine and non-serpentine strains grown reciprocally on non-serpentine and serpentine soils (Kruckeberg 1951). The non-serpentine forms proved to be much less tolerant of serpentine soil than their serpentine relatives; at least two biotypes of different physiological tolerance are present in the species. *Streptanthus glandulosus* may consequently be interpreted as a species originally possessing several edaphic biotypes, of which the non-serpentine biotypes are almost eliminated from the population, leaving the species very nearly a depleted serpentine endemic. This interpretation seems generally more plausible than that a serpentine species is extending its range off serpentine. While *S. glandulosus* appears to be only a few steps from complete serpentine endemism, such congeners as *S. breweri* Gray, *S. barbiger* Morrison (*in ed.* 1941), and *S. batrachopus* Morrison are obligate serpentine endemics.

On this basis, a reasonable, if necessarily somewhat speculative, interpretation of the development of serpentine endemism in a genus may be suggested. A species characteristic of normal soils extends its range into an area where serpentines alternate with other soil types. Among the populations of the species are some individuals at least partially adapted to low calcium levels and other conditions on serpentine; seeds of these individuals may fall on serpentine soils or the transitional soils along the margin of a serpentine area, develop to maturity, and reproduce. Among the progeny, those individuals survive that are best adapted to the environment on serpentine. In time, through this selection, various genes favorable for survival on the serpentine sites accumulate, while other genes of this originally non-serpentine population are eliminated by the selective action of the serpentine environment. The serpentine population thus develops its own genetic pattern of adaptation to serpentine environments; it becomes a biotype distinct from that on nearby non-serpentine soils within the confines of a *bodenvag* species. If, now, the non-serpentine biotypes gradually lose ground in competition with other plants until they ultimately become extinct, the species has become a depleted serpentine endemic. It has, step by step, gone through a hypothetical sequence from serpentine exclusion to serpentine endemism which appears to exist contemporaneously among the different species of a genus (*e.g., Streptanthus*).

Once established on serpentine, the species may branch out further. Occasional seeds from one outcrop or area of serpentine may reach other outcrops or areas, to which they are fairly well pre-adapted. The soils of various serpentine outcrops may be significantly different, however, and the plants growing on them may encounter somewhat different microclimates and different associates. In adaptation to these environmental differences and by genetic drift, the separated populations of the species may gradually diverge into different biotypes and eventually different "insular" species. An additional possibility is that a *bodenvag* species coming in contact with a number of serpentine outcrops may, on each, differentiate into a local biotype; and these may, with further divergence and extinction of or separation from the parent species, become local serpentine endemics. In either of these ways there may arise those clusters of closely related serpentine species, each on its own outcrop or area, which we observe in genera such as *Streptanthus*.

Interpretation of the autecology and evolution of serpentine plants requires recognition of edaphic biotypes within the species. These adaptively differentiated populations within the species, or *ecotypes,* are very well known in modern biosystematics through many studies, beginning with the pioneer work of Turreson (1922). The outstanding work of the team of Clausen, Keck, and Hiesey (1940, 1948) has shown, for example, the existence of chains of more or less discrete, climatically adapted types in various perennial species ranging from sea-level to above timberline in California. Such physiologically adapted habitat-types probably exist either as discrete populations or as complex gradients of variation in most widespread species occupying diverse habitats. Almost all the reported ecotypes have been delimited on the basis of climatic, or climatic and geographic, criteria.

The demonstration of edaphic ecotypes implies the existence of a level of ecotypic variation within the species in addition to the climatic and geographic level. The relation of the edaphic-local and climatic-geographic ecotypes may be illustrated by some of the work of Clausen, Keck, and Hiesey. In their report of transplant work on clones of the herbaceous perennial *Achillea borealis californica* (Poll.) Keck (Clausen, *et al.* 1948), the existence of climatic races in the species along an altitudinal transect was established. One of these ecotypes, that of the inner Coast Ranges and Sierra Nevada foothills, was studied by the present author (Kruckeberg 1951) in relation to serpentine and non-serpentine soils; the existence of at least two edaphic ecotypes was shown. There are thus edaphic subdivisions within climatic ones

in this species, *i.e.*, ecotypes within ecotypes. Moreover, since the geographic area occupied by the foothill climatic ecotype is very diverse lithologically and therefore is a mosaic of different soil types, additional edaphic ecotypes may very well be expected. The superposition of ecotype on ecotype at least suggests that there exists a much more complex genotypical response to the habitat than is implied in consideration of single environmental factors. Viewed from a holistic standpoint, ecotypic differentiation must be in relation to the whole pattern of selective forces in the environment. Analysis of either a climatic or edaphic ecotype by itself thus takes a segment of the species population out of context from the whole of its pattern of response to edaphic, climatic-geographic, and biotic environmental factors in relation to which its various sub-populations are maintained. To be sure, the holistic viewpoint is untenable as an experimental approach, for these various factors must be analyzed one by one. A holistic interpretation of the causes of vegetational patterning can become an experimentally substantiated concept only when analyses of each factor has been achieved and the results integrated into a unified picture.

Exclusion of Serpentine Endemics from Non-Serpentine Soils

If the preceding discussion offers some interpretation of serpentine adaptation, there remains the problem of serpentine restriction—why some species do not grow on soils other than serpentine. One possible answer would be that the serpentine endemics "need" some condition of serpentine soils. While it is hard to conceive of a plant "needing" a very short supply of calcium, serpentine plants might still conceivably be so adapted that they require high levels of magnesium, iron, nickel, chromium, or some other substance in abundant supply in at least some serpentine soils. It is easily shown by experiment that such is not the case. Plants of many serpentine species and serpentine populations of *bodenvag* types have been grown by the author and others on serpentine and non-serpentine soils. The growth of these serpentine plants is usually better on the non-serpentine than on the serpentine soils, and apparently no case has been reported in which growth of a serpentine species is inhibited by the conditions of a non-serpentine soil. While these results would have surprised some previous investigators (Novák 1928, Lämmermayr 1927, Morrison 1941), who were convinced that serpentine species were restricted to serpentine because of some essential substance furnished by that soil, it seems clear that we must seek elsewhere for the explanation of serpentine restriction.

Field observation may offer some suggestions. Even to the unpracticed eye, the demarcations between serpentine and non-serpentine vegetation, where swaths of chaparral cut through the oak woodlands, are remarkably abrupt. Such conspicuous discontinuity could conceivably be produced directly by edaphic discontinuity if the serpentine species did require some special substance in serpentine soil, but it is also suggestive of a dynamic discontinuity between kinds of individuals from different populations or species. The serpentine vegetation itself may appear from a distance to be an almost impenetrable scrub, except for the scattered bare spots. Yet, on foot in the head-high brush, one notices that each sclerophyllous bush is separated from its neighbor by a rather uniform distance. Under the shrubs and in the intervening spaces there are only scattered herbaceous plants; most of the ground surface is bare serpentine soil, lightly covered in places by dead sclerophyll leaves. The bare areas of serpentine rock appear to be truly pioneer habitats, only beginning to be occupied by plants, while the chaparral is also an "open" community with much apparently unoccupied space for plant growth. This open appearance above the soil surface does not necessarily mean that more serpentine plants can grow there than at present; the chaparral appears in fact to be in a stable and self-maintaining condition with its present population. In contrast to this open community on serpentine, however, adjacent plant communities on other soils appear "closed," having either a forest canopy, though not a dense one (in the black oak-madrone forest), or an open tree stratum with a closed herb stratum dominated by grasses (in the blue oak woodland).

A working hypothesis on the restriction of serpentine plants to serpentine thus suggests itself. The serpentine endemics are able to maintain themselves in open serpentine communities where competition is not severe, but not in the more rigorous competition of non-serpentine communities.

The first step toward an evaluation of this hypothesis would be to determine whether non-serpentine plants affect the growth of serpentine endemics when the two are grown together on a fertile non-serpentine soil. The next step—if competition, *per se*, is demonstrated in the initial step—would be to dissect the competition factor into its components. That is to say, to analyse experimentally this apparent biotic effect. Is the effect produced by competition for some factor limiting in the environment, or, as suggested by H. L. Mason (oral comm.), does some specific element of the environment (biotic, edaphic, etc.) inhibit the growth of the serpentine endemic spe-

cies? The first step should be a fairly simple one; the next step—the analysis of competition—is the difficult one. As yet, results from the first procedure only can be presented.

A rather simple procedure was followed in the first experiments. Identical mixtures of weed seed—mustard (*Brassica*), filaree (*Erodium*), perennial rye-grass (*Lolium*), bur clover (*Medicago*), wild oats (*Avena*)—and endemic *Streptanthus* seed were sown on each of two unaltered soils, a fertile Yolo fine sandy loam and unscreened serpentine soil (Henecke gravelly clay loam). These cultures were periodically irrigated, and within a week or so significant differences in the two could be detected. At maturity, the two bins had a remarkably different aspect. The Yolo bin was covered with a lush growth of mustard, bur clover, and wild oats—but not a single endemic. From a distance the serpentine bin appeared rather barren, but closer inspection showed that it was covered with a good scattering of *Streptanthus* and rather stunted growth of grasses (mostly rye-grass and wild oats). Conspicuous on the serpentine was the absence of even a single seedling of mustard, while other dicot weeds soon died. Knowing from previous greenhouse cultures that Streptanthi do well on Yolo soil by themselves, it seemed apparent that the weedy annuals in some way affected the growth of the endemics. That this is a reasonable explanation is further suggested by the fact that during the early seedling stages on the Yolo soil, several seedling Streptanthi were observed. These disappeared as the weed crop matured.

Encouraged by these results, similar competition bins (Figure 4) were set up the following year, but on a larger scale. By this time it had been established that calcium amendments to serpentine made it possible for non-serpentine plants to do well on that otherwise infertile medium. Hence, a calcium-reconstituted serpentine soil was the medium for one competition plot, in addition to the unaltered serpentine and Yolo soil bins. These three bins were sown with a mixture of weed and *Streptanthus* seed. On the unaltered soils, results identical with those of earlier experiment were observed. In addition, the expected results on the calcium-altered serpentine bin were realized. Here, mustard, clover, and filaree sprouted freely, while *Streptanthus* plants were conspicuously absent.

In these experiments with competing plants, a serpentine plant occupies a serpentine environment while its potential competitors are excluded by edaphic factors. On the non-serpentine soil, in contrast, the serpentine plant is excluded by the presence of other plants, though very well able to grow on non-serpentine soil in their absence. It would be premature to consider that these experiments fully substantiate the hypothesis offered. The "competition" should be further analyzed to determine what actual factors exclude the serpentine plants from an environment occupied by non-serpentine plants, and alternative possibilities should be further considered. An interpretation of the reciprocal exclusion of many serpentine and non-serpentine plants from non-serpentine and serpentine soils may, however, be at least tentatively offered. Some *bodenvag* species are able to range from non-serpentine onto serpentine soils because their serpentine populations, at least, are adapted

FIG. 4. Appearance of competition during seedling stage in bins. All three soil bins were sown with identical mixtures of endemic and weed seed. Bin A contains unaltered serpentine soil; Bin B, non-serpentine soil; Bin C, calcium-reconstituted serpentine soil. Note absence of *Brassica* seedlings on serpentine (Bin A), but their presence when calcium has been added to serpentine (Bin C).

to low soil calcium levels (and other factors); these species usually contain distinct serpentine ecotypes. Other species lacking these adaptations are excluded and their populations abruptly limited at the margin of the serpentine area. Still other species adapted to serpentine soils and the open serpentine communities are unable to maintain themselves against the rigorous competition of non-serpentine plant communities; their distributions are consequently terminated along the same serpentine border, though by dynamic or biotic, rather than simply edaphic factors. Perhaps on this basis the contrasts and discontinuities so impressive in the foothill mosaic of woodland and chaparral may be understood.

Summary

1. In California, the chaparral vegetation on serpentine includes some genera of annual herbs that show a striking development of serpentine endemism and provide material for its study.

2. Experimental results are reported which support those of Walker (1954) in showing that tolerance of low calcium levels is a principal adaptation required for growth of plants on serpentine soils. *Bodenvag* species occurring both on and off serpentine are able to do so because their serpentine populations are adapted to low calcium levels. It is shown that in most cases the population on serpentine is ecotypically distinct from that on non-serpentine soils.

3. All degrees of serpentine tolerance appear in the genus *Streptanthus*. Adaptation to serpentine followed by "biotype depletion" (Stebbins 1942), and the development of some isolated populations into "insular" endemics provide reasonable evolutionary explanations for serpentine endemism.

4. Experiments are reported showing that serpentine plants may be restricted to serpentine by intolerance of the more rigorous competition in non-serpentine plant communities. Thus, edaphic factors on the one hand, biotic or dynamic factors on the other, may produce the sharp discontinuities between serpentine and non-serpentine vegetation.

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THE ECOLOGY OF SERPENTINE SOILS

IV. THE VEGETATIONAL RESPONSE TO SERPENTINE SOILS[1]

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The distinctiveness of serpentine vegetation has been indicated in the preceding papers. Although the types of serpentine vegetation in different parts of the world are diverse, some common characteristics or tendencies may suggest themselves when serpentine vegetation is in each case compared with adjacent vegetation on other soils. As a basis for considering these tendencies, a particular area of serpentine vegetation, that of the Siskiyou Mountains of southwestern Oregon, will be treated in detail. The present paper will discuss Siskiyou serpentine vegetation first in terms of populations and vegetation structure, or physiognomy, and second in terms of flora or species composition, and will then seek to interpret the vegetational response to serpentine soils.

Just north of the California-Oregon boundary, west from O'Brien, Oregon, is one of the extensive areas of serpentine vegetation in the Siskiyou Mountains, occupying an almost continuous area of more than 150 square miles of peridotite and serpentine (Wells *et al.* 1949). Across the Illinois Valley from it, in and near the Oregon Caves National Monument, "typical" vegetation for the area occurs on quartz diorite and other rocks. A comparison of vegetation in these two areas formed the basis of the study. So different are their vegetations that one might imagine one had traveled to another part of the continent in crossing the few miles from the diorite area to the serpentine, if it were not difficult to think of another area much resembling the Siskiyou serpentines. The mountains of diorite and other rocks east of the Illinois Valley are covered by dense evergreen forests and are valuable timber lands for the Douglas fir and Port Orford cedar these forests contain. Pines and other conifers in open, stunted stands, which the loggers are generally content to leave alone, occupy the serpentine area. Both too steep and too infertile for farming, the serpentine mountains are almost without present economic value except for limited grazing and mining.

The approach of gradient analysis (Whittaker 1951, 1952, *cf.* Curtis and McIntosh 1951, Brown and Curtis 1952) was used for the study. Vegetation site-samples were taken at random, so far as possible, over the mountain surface. Each sample included a stand-count of trees for 0.1 or 0.2 hectare, undergrowth counts for 25 square-meter plots, and data on soil material, topographic position, and location. Fifty of these samples for undisturbed stands in each area at elevations between 2,000 and 3,000 feet were used in the tabulations. The samples were first arranged into transects by topographic position, and the plant species were grouped into four classes, from mesic to xeric, on the basis of the positions of their populations along the moisture gradient. Weighted averages of stand composition based on these classes give a more sensitive expression of the moisture relations of stands (*cf.* Curtis and McIntosh 1951, Brown and Curtis 1952). Using these weighted averages, the samples were arranged in series from most mesic to most xeric and grouped into ten sets of five samples each along the moisture gradient. The resulting tables[2] showing the change in plant populations from most mesic ravines to most xeric southwest slopes on diorite and on serpentine are the basis of the following comparison and interpretation of these vegetations.

DESCRIPTION OF DIORITE AND SERPENTINE VEGETATION

In the diorite area, well-developed, closed mountain forests prevail. In ravines Douglas fir, *Pseudotsuga taxifolia* (Lamb.) Britt., and Port Orford cedar, *Chamaecyparis lawsoniana* Parl., dominate the stands, with a low-tree stratum in which deciduous species are more important than

[1] A contribution from the Department of Zoology, Washington State College, completed before joining General Electric Co. This study was supported in part by the funds for biological and medical research of the State of Washington Initiative Measure No. 171. The author is much indebted to M. Ownbey and A. Cronquist for determining the specimens of the difficult flora of the Siskiyous; the voucher specimens have been deposited in the herbarium of Washington State College. All three authors are indebted to H. L. Mason and W. D. Billings for critical readings of the manuscripts before they were submitted for publication.

[2] A monograph on the vegetation of peridotite, olivine gabbro, and quartz diorite is in preparation. Since it is expected that data for the three transects will be presented together at that time, the extended tables for two of the soil materials are not given with this shorter account.

sclerophylls. *Gaultheria shallon* Pursh and *Berberis nervosa* Pursh are important shrubs, occurring along with a variety of mesic herbs of wide distribution. As one proceeds from these ravines to northerly and easterly slopes, Port Orford cedar and the other species mentioned, except Douglas fir, gradually decrease in numbers until no longer present. In the absence of cedar, Douglas fir is the canopy dominant (with some *Pinus lambertiana* Dougl.) above a dense lower tree-stratum of sclerophyllous trees, mainly tanoak, *Lithocarpus densiflorus* (H. & A.) Rehd. As one follows the moisture gradient from intermediate slopes to xeric southerly ones, the Douglas fir canopy becomes more and more open until, on the driest slopes, these large trees are only scattered above a canopy of sclerophylls including canyon liveoak, *Quercus chrysolepis* Liebm., chinquapin, *Castanopsis chrysophylla* Dougl.) A. DC., and madrone, *Arbutus menziesii* Pursh, as well as tanoak (Fig. 1). Undergrowth coverage in the diorite stands is low, except in mesic sites. In general character, the diorite vegetation is a pattern of closed forests dominated by Douglas fir and the sclerophylls, with progressive change from Douglas fir, Port Orford cedar, and deciduous species in more mesic sites toward stands of sclerophylls with Douglas fir in more xeric ones.

Port Orford cedar and Douglas fir appear also as dominants at the mesic extreme of the pattern on serpentine, but form open stands of smaller trees along with western white pine, *Pinus monticola* Dougl., and other species (Fig. 2). *Rhododendron occidentale* (T. & G.) Gray is the most important shrub. The herb stratum shows an unusual mixture of rare serpentine species (*Trillium rivale* Wats., *Lilium howellii* Johnst., *Cypripedium californicum* Gray) with more familiar species from bogs and marshes (*Darlingtonia californica* Torr., *Rudbeckia californica* Gray, *Helenium bigelovii* Gray, *Tofieldia glutinosa* spp. *occidentalis* (Wats.) C. L. Hitchc.). In intermediate sites, mixed stands of Douglas fir, white pine, sugar pine, *P. lambertiana* Dougl., Jeffrey pine, *P. jeffreyi* Grev. and Balf., and incense cedar, *Libocedrus decurrens* Torr., occur (Fig. 3), with a rather dense stratum of shrubs (*Quercus chrysolepis* var. *vaccinifolia* (Kell.) Engelm., *Lithocarpus densiflorus* var. *montanus* (Mayr.) Rehd., *Vaccinium parvifolium* Smith, *Arctostaphylus nevadensis Gray*, an unnamed shrubby variant of *Umbellularia californica* Nutt., *Rhamnus californica* var. *occidentalis* How., *Garrya buxifolia* Gray, *Rosa gymnocarpa* Nutt., *Berberis pumila* Greene, and *Amelanchier gracilis* Heller). This shrub layer is dominated by sclerophyllous species, many of them shrubby varieties of the sclerophyllous trees of

FIG. 1. A xeric stand on quartz diorite, open south slope above Grayback Creek, Siskiyou Mountains, southwestern Oregon, at 2300 ft. elev. *Pseudotsuga taxifolia* with *Lithocarpus densiflorus, Quercus chrysolepis,* and *Arbutus menziesii; Pinus lambertiana, Rosa gymnocarpa, Boschniakia hookeri* Walp., and *Apocynum pumilum* (Gray) Greene present. October 10, 1951.

diorite or shrubby congeners of these trees. The tree layer, however, is almost entirely coniferous. The broadleaved trees so important on diorite are conspicuous by their absence from serpentine, except for occasional madrones. It is as if, with the opening and reduction in size of the forest on serpentine, the broadleaf tree stratum had been dwarfed to a shrub layer.

In more mesic sites, shrub coverage may be 80 per cent or more, with scattered open patches of grass; but in more xeric sites, the shrubs themselves occur only in scattered patches. The undergrowth of intermediate sites on serpentine has a distinct two-phase structure which is often con-

FIG. 2. A mesic stand on serpentine in a ravine near the Wimer Road, Siskiyou Mountains, southwestern Oregon, at 2100 ft. elev. *Chamaecyparis lawsoniana, Pinus lambertiana,* and *P. monticola, Rhododendron occidentale, Darlingtonia californica, Helenium bigelovii, Lilium occidentale* Purdy, *Carex* spp. July 21, 1951.

FIG. 3. An intermediate stand on serpentine on an open east slope of Josephine Mtn., Siskiyou Mountains, southwestern Oregon, at 3800 ft. elev. *Pinus monticola* with *Libocedrus decurrens* and *Pinus jeffreyi;* shrub coverage 50 per cent with *Quercus chrysolepis* var. *vaccinifolia* predominant, *Rhamnus californica* var. *occidentalis,* and *Garrya buxifolia.* July 20, 1950.

spicuous in sampling quadrats along a tape; the sampler finds himself working in shrubs for a few meters, then in grass, then back in shrubs. As if to make this two-phase structure the more apparent, there is a reversal of phase along the gradient. The shrubs form the continuous phase in the more mesic sites but decrease along the moisture gradient while the grass increases, until the shrubs are the discontinuous phase in the grass of more xeric sites. The tree and herb populations respond to the difference of environment of the two phases. While the same tree species grow in both, there is a difference of relative abundance in the two phases probably determined by effects of the different undergrowth environments on seedling survival. The more mesic tree species, Douglas fir, white pine, and sugar pine, tend to be concentrated in the shrub phase and the more xeric Jeffrey pine in the grass phase, while incense cedar shows no clear preference.

The shrub stratum just described is absent from most xeric sites, and here the whole vegetation resembles the grassy phase of subxeric sites. Jeffrey pine is the dominant tree, often with no other species but incense cedar present, and forms a very open stand above a grassy floor (Fig. 4). The community is thus a woodland or "temperate savanna," which perhaps may best be described as pine steppe and compared with similar communities formed by *Pinus sylvestris* and other species in Europe. Scattered *Arctostaphylos viscida* Parry may appear as a high shrub stratum, with *Con-*

FIG. 4. A xeric stand on serpentine on an open southeast slope above Rough-and-Ready Creek, Siskiyou Mounains, southwestern Oregon, at 1900 ft. elev. *Pinus jeffreyi* with *Libocedrus decurrens* and *Pseudotsuga taxifolia;* sparse shrub coverage of *Arctostaphylos viscida* with *Quercus chrysolepis* var. *vaccinifolia* and *Umbellularia californica; Xerophyllum tenax* (Pursh) Nutt. and grass spp. The soil is rockier and less developed than in most similar stands. July 17, 1950.

volvulus polymorphus Greene and *Rhamnus californica* var. *occidentalis* the only other shrub-layer species present. The grasses are widespread *bodenvag* species; *Stipa lemmoni* (Vas.) Scribn. and *Sitanion jubatum* J. G. Sm., are usually most important. Among the herbs other than grasses are some of the many Siskiyou and Klamath endemics of the serpentine area. A few of these endemics which occur with square-meter frequencies of 5 per cent or more for the whole transect (*Vancouveria chrysantha* Greene, *Lomatium howellii* (Wats.) Jeps., *Galium ambiguum* Wight, *Iris bracteata* Wats., *Hieracium cynoglossoides* var. *nudicaule* Gray, *Sanicula peckiana* Macbr., *Horkelia sericata* Wats., and the prostrate *Ceanothus pumilus* Greene) may be mentioned as most important.

The pattern of low-elevation serpentine vegetation is thus one in which pine species share dominance with other conifers in the open stands of small trees, a pattern which changes continuously along the moisture gradient from Port Orford cedar-white pine-Douglas fir stands in ravines, through mixed pines and Douglas fir with two-phase undergrowth in intermediate sites, to the Jeffrey pine steppe on xeric slopes. The contrast with the diorite vegetation pattern may be illustrated by a transect diagram (Fig. 5) as well as by photographs. The Douglas fir-sclerophyll forest on diorite (the Mixed Evergreen Forest of Munz and Keck 1949) is a widespread vegetation type of the Klamath Mountain region and northern Coast Ranges. The Jeffrey pine steppe of xeric serpentine sites is, in superficial appearance, part of a vegetation type of even wider range, the yellow pine steppes dominated by *Pinus ponderosa* and relatives. The remaining serpentine vegetation types, however, are as distinctive and anomalous in vegetation structure as in floristics.

Exclusion of growth-forms important on one soil from the vegetation on the other is responsible for much of the contrast of diorite and serpentine vegetation. The broad-leaf trees are absent or represented only by shrubs on serpentine; the pines (except sugar pine), grasses, and characteristic sclerophyllous shrubs of serpentine are absent or of minor importance on diorite. Some further basis of the contrast may be seen in the effects of serpentine on the population of Douglas fir. The average population density of this tree on serpentine is less than half that on diorite, comparing the whole transects (average number of stems 1 inch and above d.b.h. per hectare, 177 on diorite vs. 78 on serpentine). The trees on serpentine are, furthermore, noticeably smaller. Increment borings indicate a growth rate on serpentine about two-thirds that on diorite (average diameters at 100th ring, breast height, of 11.4 inches for 20 diorite stems, 7.4 inches for 5 serpentine stems). With the sclerophyllous trees nearly excluded and Douglas fir kept to a low population of small trees, the serpentine stands are necessarily open ones.

The Floristics of Serpentine and Diorite

The species listed for the two transects may provide a basis for floristic comparison also. When species which occur only once or twice in the fifty samples of a transect are excluded, about a hun-

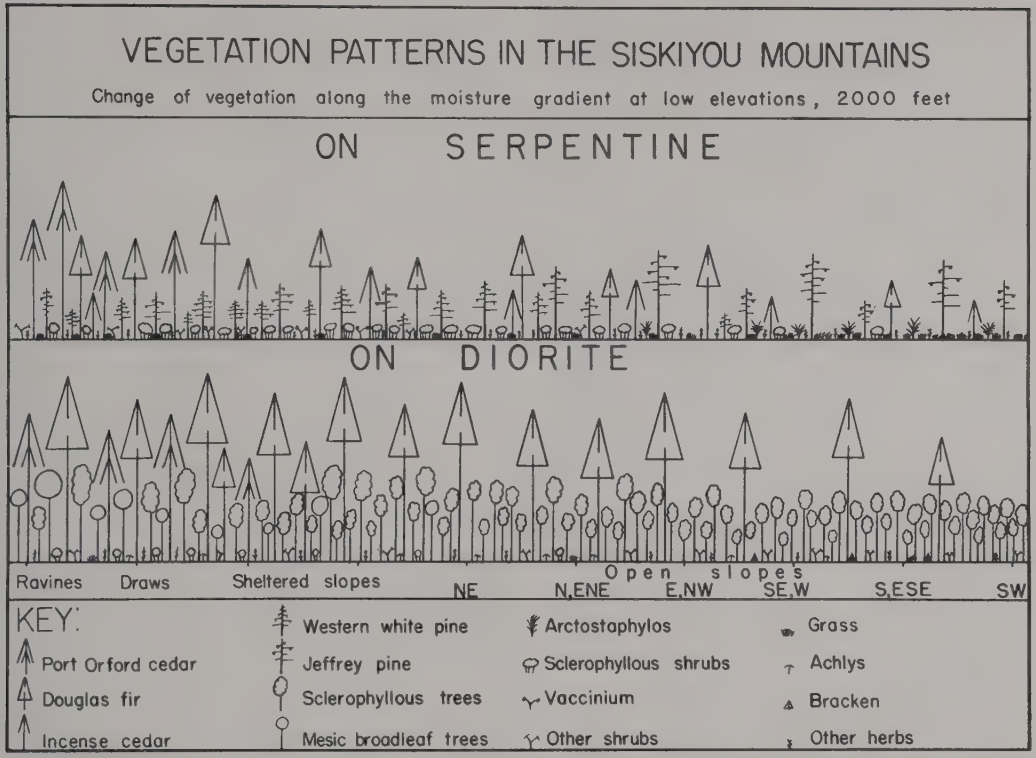

FIGURE 5. Transect diagrams of vegetation patterns on serpentine and on quartz diorite, from most mesic sites on left to most xeric sites on right, Siskiyou Mountains, southwestern Oregon.

dred species remain for each—101 on diorite, 113 on serpentine. These numbers may indicate well enough that the vegetation on Siskiyou serpentines is by no means floristically impoverished. The breakdown of the two floras in terms of major growth-forms (Table I) shows a more evident contrast. Half as many tree species maintain themselves on serpentine as on diorite; all but one of these are conifers and four of them are pines. The number of shrub species is reduced slightly on serpentine; but the greatest change in composition of this stratum is the dominance on serpentine of the evergreen-sclerophyllous shrubs, which are a minority on diorite. The herb stratum on serpentine is distinctly richer floristically than on diorite, and includes about twice as many grasses and sedges.

TABLE I. *Floristic measurements of range and area for serpentine and diorite floras in the Siskiyou Mountains. Based on 113 serpentine and 101 diorite species occurring in the low-elevation composite transects. Diorite left; serpentine right (bold face)*

	Grasses & sedges		Other herbs		Shrubs		Trees		Total	
Number of species	8	**17**	58	**71**	19	**17**	16	**8**	101	**113**
Number of endemics	0	**0**	2	**25**	0	**5**	0	**0**	2	**30**
Extent: North	4.4	**3.3**	3.7	**1.9**	3.6	**1.6**	3.2	**2.6**	2.6	**2.1**
East	4.2	**3.9**	3.1	**1.9**	2.5	**1.7**	2.2	**2.4**	2.8	**2.2**
South	2.9	**3.0**	2.8	**1.7**	2.6	**2.2**	3.1	**3.6**	2.8	**2.1**
Direction of greatest extent: North	3	**4**	27	**19**	13	**3**	7	**2**	50	**28**
East	3	**8**	12	**8**	0	**0**	0	**0**	15	**16**
South	0	**4**	7	**19**	4	**9**	6	**4**	17	**36**
Indeterminate	2	**1**	12	**25**	2	**5**	3	**2**	19	**33**

The extent of the floristic contrast may be further shown by some such measure as Jaccard's (1912, 1932) coefficient of community. Of the lists of 101 and 113 species, 22 are shared of a total of 192 species occurring in either or both. A coefficient of $100 \times 22/191 = 11.5\%$ results, a value which is surely phenomenally low for two areas of vegetation a few miles from each other under the same general climate. Comparing various districts of Switzerland, Jaccard (1932: 171) obtained values ranging from 50% to 56%, comparing floras of gneiss and limestone soils in one district produced a value of 48%. Use of species lists as large as Jaccard's (300 or more), taken for all elevations and soils on opposite sides of the Illinois Valley would raise the coefficient but ob-

scure the real contrast of diorite and serpentine floras at comparable elevations. Since, as shown by Kruckeberg (1954), the populations of most *bodenvag* species are distinct, the actual percentage of ecotypic populations which are shared by the two vegetations within the limits of the study areas is well below 11.5%.

A breakdown by floristic areas further illustrates the contrast (Table II). The extent of narrow endemism for which serpentine vegetation is perhaps more celebrated than any other feature is at once apparent. Seventeen of the serpentine species are restricted to the narrower area of the Siskiyou Mountains along the California-Oregon border; thirteen others are restricted to the broader Klamath Mountain region of northern California and southern Oregon. These are a small fraction of the narrow endemics of serpentines and other soils in the Siskiyous. In the diorite transect, a single Siskiyou endemic appears (*Tauschia kelloggii* (Gray) Macbr.) Half of the diorite flora (50%) is made up of widespread western and nearctic species. These are reduced to 30% in the serpentine vegetation, in which the endemics together with the less widespread Sierran and Coastal groupings made up the majority.

TABLE II. *Representation of floristic areas in serpentine and diorite floras, Siskiyou Mountains. Percentages in various floristic groupings of 113 serpentine species and 101 diorite species occurring in the low-elevation composite transects*

Floristic grouping	Serpentine	Diorite
Siskiyou endemic	15	1
Klamath endemic	12	1
Cascadian	2	1
Sierran	11	4
Sierra-Cascadian	3	8
Sierra-Coastal	10	6
Coastal	17	29
Western	21	34
Nearctic	9	16

A further means of expressing some floristic features quantitatively has been developed for this comparison. The range of each species was expressed in terms of the distance of its extent north, east, and south of the Siskiyous, by a scale in which 0 indicated restriction to the Siskiyous in a given direction, 1 restriction to the Klamath Mountain region, and each further unit a 200-mile interval to the limits of the continent. The contrast in average extent of range is at once apparent (Table I). In the grouping of herbs other than grasses, the diorite flora has almost twice the average extent in a given direction, hence almost four times the average area of distribution. A similar contrast appears among the shrubs but is less apparent in the other two growth-forms. The designations "Californian" and "Northwestern" were not considered very meaningful for the breakdown of Table II, but the contrast in direction of greatest extent is revealing. Numbers of species with their greatest extent of range to the north or to the south may be compared in Table I. About twice as many species have their greatest range to the north on diorite as on serpentine, and about twice as many species have their greatest range to the south on serpentine as on diorite. In this sense, the serpentine flora may be described as Californian and the diorite flora as Northwestern in affinities, although both occur in the floristic center lying between these two regions.

Successional Status of Serpentine Vegetation

It has been one of the assumptions of the climatic climax theory (Clements 1928, 1936, Phillips 1934-5, Cain 1939) that the distinctive vegetation of special soils is seral or successional and, given time for development of soil maturity, will converge to essential identity with the climatic climax vegetation on more typical soils (Clements 1928: 284-5, Cain 1939: 150, Daubenmire 1947: 55). This assumption implies that much or all of the physiognomic and floristic pecularity of serpentine vegetation should disappear when it reached the climax. It further suggests that the normal process of ecological succession should develop mature soils on serpentine as productive as soils developed from other rocks. Criticisms of the climatic climax theory have been considered elsewhere by the author (Whittaker 1951, 1953). Without reviewing these here, the following evidences on whether the Siskiyou serpentine vegetation is seral or climax may be adduced:

1. Seedling data from undergrowth quadrat counts show that the dominant trees on serpentine are reproducing (except knobcone pine, *P. attenuata* Lemm.). There is no evidence that the sclerophyllous trees of diorite are effectively entering the serpentine stands, as trees. The size-distributions of trees on serpentine show the J-curve form (Meyer and Stevenson 1943) of self-maintaining stands (except knobcone pine and Jeffrey pine steppe). The serpentine vegetation shows the characteristics of self-maintenance to be expected of vegetation stabilized in relation to its site.

2. The soils on both diorite and serpentine are shallow and rocky soils of mountain slopes, and there is no evidence that those on serpentine are less mature than those on diorite. Valley and outwash serpentine soils along the western edge of the Illinois Valley support serpentine vegetation.

3. Islands or exclaves of each rock in the area of the other show the persistence of differences in vegetation. Islands of other soils in the serpentine area support sclerophyllous trees or Douglas fir-sclerophyll stands. Islands of serpentine in the diorite area bear open stands dominated most frequently by knobcone pine and Jeffrey pine, which are serpentine species in the areas studied, and have serpentine undergrowth flora, the extent of development of which seems roughly proportional to extent of the outcrop and proximity to major serpentine areas.

4. The stand-to-stand regularity or predictability of patterning (Whittaker 1953) indicates that serpentine vegetation is stabilized, so that similar climax populations have been established in similar sites.

5. Successions in the two areas are different. Plants of bare serpentine rock and exposed serpentine soil are, as indicated by Kruckeberg (1954), serpentine plants together with some *bodenvag* grasses; such sites in the diorite area bear more familiar plants of newly exposed or disturbed situations. Recent, more severe burns are indicated on diorite by dense young stands of sclerophyllous trees, but on serpentine by stands of knobcone pine.

These lines of evidence point uniformly toward the same conclusion: Siskiyou serpentine vegetation is not a seral stage to the vegetation of other soils but is a distinctive climax of its own distinctive successions. Conclusions on climax status must allow for the extent of past fires in the Siskiyous; both the diorite and serpentine vegetations have been burned. In the dry-summer climate of this area, light summer fires are part of the environmental complexes in relation to which the present vegetations of both areas have developed. Only some stands, affected by more severe fires, are clearly successional. Allowing for the effects of fire, the author would interpret the serpentine vegetation of the Siskiyous as a complex and fully developed climax pattern in its own right, part of the still more intricate pattern of vegetation on serpentine, diorite, gabbro, and other rock types represented in the Siskiyou Mountains. Whatever the interpretation according to the three climax hypotheses (Whittaker 1953)—as a stabilized edaphic sub-climax, as one of a number of edaphic climaxes of the area, or as a climax pattern itself—, there is no reason to believe that the Siskiyou serpentine soils and vegetation are becoming more like those of surrounding, economically more valuable areas.

Interpretation and Conclusion

Impressive as some of the contrasts of serpentine and non-serpentine areas are individually, it seems appropriate to try to draw together these details of the three papers in concluding the symposium.

It was shown by Walker and Kruckeberg that a deficiency of calcium underlies the effects of serpentine soils. With due allowance for other peculiarities of serpentine soils, and for the individuality of both serpentine soils and plant species, we may consider the nutrient deficiency, especially of this element, as the most crucial and general characteristic of serpentine soils affecting plants.

Plant species encountering serpentine soils within their ranges show various distributional responses, ranging from complete exclusion from serpentine to complete restriction to serpentine. Species retricted to serpentine are characterized by tolerance of the low calcium levels in these soils. Some *bodenvag* species naturally tolerant of low calcium levels may be able to grow on serpentine without ecotypic differentiation; but most plant species, as Kruckeberg has shown, are able to occupy serpentine habitats only as distinct edaphic ecotypes. The physiological adaptation of these serpentine plants to low calcium levels and other peculiarities of serpentine habitats is often expressed morphologically, in serpentinomorphism.

When species occur both on and off serpentine soils, the non-serpentine populations may in time lose out in competition with other plants, leaving the serpentine populations isolated on their soil. Many serpentine species have probably become, or are becoming, serpentine endemics by this process of "biotype depletion." Other endemics have arisen as "insular" species by the differentiation of a local, serpentine-adapted population from the population of a parental species. Kruckeberg's experiments indicate that in either case, these endemics are probably restricted to serpentine by their intolerance of the more rigorous competition on other, more typical soils. As may often be the case with the populations of special or extreme habitats, these are able to survive in environments of especially exacting physical conditions to which they are adapted, but are unable to compete elsewhere with other species which are excluded by those conditions.

While each species responds to serpentine soil according to its own potentialities, some relative differences of response among plant growth-forms appear. The experimental data of Kruckeberg and the field data of the author indicate that grasses are more easily able to occupy serpentine environments than are many other herbs and suggest that some grass species may do so without ecotypic differentiation. The field data for coniferous trees suggest they may occupy serpentine

habitats with the same facility; all the diorite conifers except *Taxus brevifolia* Nutt. (as a shade-plant necessarily excluded from serpentines in this area) occur also on serpentine. Deciduous trees are virtually excluded from Siskiyou serpentines; and, although stands of oaks and other deciduous trees occur on serpentine in some areas, deciduous forests on serpentine are on the whole much less extensive than coniferous stands. The evergreen-sclerophyllous shrubs appear more successful than deciduous shrubs on serpentine in the Siskiyous and in most, but not all, other areas. Although these can be only tendencies, it may be suggested that the needle-leaved or coniferous trees (and especially pines), evergreen-sclerophyllous shrubs, and grasses (and sedges) succeed more generally on serpentines than broad-leaf trees, broad-leaved deciduous shrubs, and many broad-leaved herbs. Most serpentine vegetations throughout the world appear to be dominated by some one or by some combination of these three adaptable growth-forms —coniferous trees, sclerophyllous shrubs, and grass-like plants.

The physiognomy of serpentine vegetation may further be understood on the basis of stunting or impoverishment of growth, referred to by all three authors. The reduction of both population level and growth rate in Douglas fir on serpentine has been mentioned; from this and the exclusion or reduction to shrubby equivalents of the broad-leaved trees, the stunted, open appearance of Siskiyou serpentine vegetation results. The openness of the tree stratum permits species intolerant of the shade of a closed canopy to reproduce; thus several pine species are able to maintain populations on serpentine. The sparse canopy coverage permits much light to reach lower strata, and may also imply a reduced demand on the available soil water by the trees. A development of undergrowth far beyond that on diorite is thus possible. Floristically, the undergrowth on serpentine in the Siskiyous is richer in species than that on diorite; in relation to physiognomy, the serpentine undergrowth is of greater coverage and more massive.

Similar physiognomic effects appear in other serpentine vegetations which have been described, almost all of them from forest climates. Sparse alpine meadow or tundra-like communities (eastern Canada and Scandinavia, Fernald 1907, 1911, Rune 1953) and open coniferous stands (north Urals, Sočava 1927) occur in northern forest or taiga regions. In temperate lower latitudes, serpentine vegetations include pine steppe (Europe, Beger 1922-3, Suza 1928, Zlatník 1928a, Kretschmer 1931, Markgraf 1932, Bargoni 1943; Japan, Kitamura and Momotani 1952, Kitamura and Murata 1952, Yamanaka 1952; eastern United States, Radford 1948; and Oregon, present paper) and other open coniferous stands (Washington and Oregon; south Urals, Iljinski 1936; Spain, Palacios 1936; Japan, Yamanaka 1952), deciduous forest (Yugoslavia, Pančič 1859; Albania, Markgraf 1932; eastern United States, Harshberger 1903, 1904, Pennell 1910, Radford 1948) and deciduous shrubs (Japan, Yamanaka 1952), chaparral (California), live-oak (Spain, Palacios 1936), and *lande* (France, LeGendre 1919), and edaphic steppe (Italy, Messeri 1936, Pichi-Sermolli 1948; Czechoslovakia, Suza 1928; eastern United States, Pennell 1910, Braun 1950: 248). In tropical climates, serpentines support savanna (Karakelang, Lam 1927; Cuba, Carabia 1945, Beard 1953), and scrub (New Caledonia, Däniker 1939, Birrell and Wright 1945; Cuba, Seifriz 1940). In south temperate New Zealand, luxuriant *Nothofagus* forests are replaced on serpentine by tussock grassland and shrub communities (Betts 1918, Cockayne 1921). The physiognomic types on serpentine are varied; but in each of these the tree stratum is reduced and the lower strata increased, compared with vegetation on other adjacent soils: the concentration of plant life in the community moves down one or two stories.

It is familiar that increasingly favorable environments (moisture and temperature especially) permit increased closing, elevation, and differentiation into strata of the community (Dansereau 1951: 219). In serpentine vegetation we see the generalization in reverse: with less favorable environment (nutrients) there is opening, lowering, and reduction of the community toward the lower strata. Differences in relative productivity of natural communities and relative amount of plant life or biomass maintained in them must underlie these phenomena. Increasingly favorable conditions of temperature, moisture, and nutrients permit increasing community productivity and with this increasing development of community structure from the lower strata upward.

There is thus a very rough parallelism in the effects of decreased moisture, temperature, and nutrients on vegetation structure, to which may be related another peculiarity of serpentine vegetation. Serpentine vegetation is xeromorphic. In the morphology of some of its species and in the morphology of the vegetation itself it shows some of the marks of adaptation to dryness. In the various occurrences of serpentine vegetation cited, the serpentine vegetation is in each case a step more xeric in appearance than vegetation on other soils. Physical characteristics of serpentine soil described above by Walker (1954) may contribute to the dryness of serpentine habitats; but in some cases; as in the Siskiyous, physical characteristics

of serpentine and non-serpentine soils are similar. Since the serpentine vegetation occurs side by side with other vegetation, receiving the same rainfall, its physiognomic response may best be interpreted as a pseudo-xeromorphism. The effects of decreased moisture are simulated by the effects of decreased nutrients, because basic productivity is reduced in both cases and because some of the same plant growth-forms are adapted to both dryness and infertility.

Characteristics of vegetation which parallel these in part, although in response to different edaphic factors, appear on some other special soil parent-materials: gypsum (Dziubałtowski 1923, 1926, Weiss 1924, Mrugowsky 1931, Sokolowa 1935, Leontjev 1935, Emerson 1935, Campbell and Campbell 1938, Meusel 1939, 1941, Johnston 1941, Waterfall 1946, Braun-Blanquet 1951, Gilliland 1952) and magnesite (Lämmermayr 1928a, 1928b, 1933, 1934, 1935, Björkman 1937), some dolomites and limestones, as in the cedar glades of eastern North America (Harper 1926, Freeman 1933, Erickson *et al.* 1942, Quarterman 1950a, 1950b) and European edaphic steppe and pine steppe from Balkan *Karst* north to Baltic *Alvar* vegetation (Turrill 1929, Allorge 1921-2, Kaiser 1926, Dziubałtowski 1926, Zlatník 1928a, Kozłowska 1928, Gams 1930, 1938, Klika 1932, 1933; Du Rietz 1923, Sterner 1925, Vilberg 1929, Jalas 1950, Albertson 1950), Appalachian shale barrens (Steele 1911, Wherry 1930, Core 1940, Allard 1946, Platt 1951), zinc and copper soils (Schwickerath 1931, Robyns 1932, Braun-Blanquet 1951, Rune 1953), Australian soils low in phosphate (Beadle 1953), porphyry hills in Germany (Meusel 1940), and altered andesite in Nevada (Billings 1950). One notable reversal of the tendency for serpentine vegetation to be of reduced stature compared with the vegetation of other soils appears where two of these edaphic vegetation types meet on the Greek island of Euboea—*Karst* steppe on limestone and pine forest on serpentine (Boydell 1921, Turrill 1929). To varying degrees these other vegetations of special soils also resemble serpentine vegetation in floristic peculiarity and occurrence of endemic species. Rune (1953) has recently suggested that relict and paleoendemic species tend to be more characteristic of soils of high calcium or magnesium content (serpentine, magnesite, limestone and dolomite, gypsum), neoendemic populations of soils characterized by heavy metals—nickel (serpentine), zinc (calamine), copper, and perhaps others. As serpentine soil combines chemical properties of both groups of soils, so serpentine floras include both paleoendemics and neoendemics (Rune 1953: 108).

Rune's description of serpentine communities across the North Atlantic from one another also illustrates a major contrast in the floristics of serpentines in far-northern and southern regions. The serpentine communities of Scandinavia and eastern Canada are relatively poor in numbers of species and extent of narrow endemism, compared with southern serpentine areas. In the western United States, the serpentine vegetation of Washington is not floristically rich and includes few, if any, narrowly endemic species. The major serpentine areas from the Siskiyou Mountains south into California are floristically rich and are remarkable for the extent of narrow endemism among their species, as are tropical serpentines still farther south. It is possible that contrast between serpentine and non-serpentine soils is less marked in humid far-northern climates. Serpentine rocks are of varied chemical properties and are subject to processes of soil-formation which differ in different climates. The relative importance of endemics vs. *bodenvag* species among serpentine floras may presumably be partly correlated with the extent of contrast between serpentines and adjacent soils (and hence the degree to which serpentine areas represent environmental extremes, Detling 1948).

It is also true that the northern serpentine areas have been exposed to glaciation, and there has consequently been much less time for the processes described by Kruckeberg to produce endemic serpentine species and distinctive serpentine ecotypes. The surrounding, non-serpentine floras of the northern regions are less rich, and hence offer a smaller stock of species from which these processes can, in time, produce distinctive serpentine floras. The northern serpentine areas are also relatively small (though some are larger than some southern areas with rich serpentine floras), and the extent of development of serpentine floras is partly related to extent of serpentine areas. The information on serpentine floras permits no real evaluation of the signicance of extent of serpentine area, time the serpentine surface has been exposed, and richness of surrounding flora. The information is not inconsistent, however, with the possibility that both richness in species and extent of endemism in serpentine floras are partially correlated with each of these. Age, area, and richness in species are not causal factors affecting plant populations (Mason 1946a), but may have indirect relations with the number of species which occupy a serpentine area as ecotypes and endemics. It is of interest to compare these considerations on the floras of serpentines, as edaphic islands, with those on the floras of oceanic islands (Szymkiewicz 1938, Cain 1944: 215-21, Mason 1946a).

The physiognomic distinctiveness of serpentine

vegetation may suggest some further interpretation of its floristic peculiarities. The openness of serpentine vegetation implies penetration of more light to the lower strata, greater exposure to air movement and evaporation, exposure to higher afternoon temperatures, and retention of heat by the exposed rocks and soil. Any autecological interpretation of the Siskiyou serpentine flora described here must allow for this contrast in light, evaporative, and temperature conditions. Microclimates around the foliage of herbs and shrubs on serpentine are at times drier, and tend to induce greater loss of water by transpiration, than microclimates within the forests on diorite. Possession of morphological characteristics of growth in dry and exposed conditions by species of drier serpentine sites may thus be no accidental imitation of xeromorphism. To the warmer and drier conditions in communities of serpentine and other special soils may be related also the xerothermic character of some of their relict species and the interpretation of some of these communities as xerothermic in character by European authors (Suza 1921, 1935, Gams 1930, Sillringer 1931, Klika 1933, Meusel 1939, 1940, 1941).

The necessity of considering environmental factors as parts of a complex has been indicated by Kruckeberg and recently stated by Billings (1952). If we consider environment and natural community together as forming the ecosystem, then serpentine vegetation offers an *ecosystemic* environment differing widely in edaphic, microclimatic, and biotic characteristics from that on diorite. On this basis, we may understand why so few species have succeeded in bridging, even with ecotypic differentiation, the diverse and fundamental differences between diorite and serpentine habitats within the limits of the study areas. We may also understand, however, why a number of species which have failed to occupy both soils within these limits have been able to do so elsewhere under different conditions. Thus a number of the Siskiyou "serpentine species" of this study occur on non-serpentine soils in drier or more exposed habitats at higher elevations, farther east in the Siskiyous, or farther south into California. On the other hand, a number of "diorite species" excluded from serpentine at lower elevations enter denser forest stands on serpentine at higher elevations. The fundamental contrast in total-environment thus may provide a better explanation than edaphic difference alone for the low coefficient of community obtained and for the contrast in per cent of endemism and extent of average range in the two floras. The contrast in total-environment may also account for the difference in floristic affinities between the serpentine flora and the shade plants of the diorite forests. Even apart from species shared with serpentine chaparral in California, we might expect more of the species of open serpentine vegetation to extend southward into the drier woodland, chaparral, and grassland vegetation of California, more of the species of closed forests on diorite to extend into mesophytic forests of the Northwest.

The natural communities on serpentine and diorite differ in almost every feature we can describe or measure. Underlying their various contrasts is a fundamental difference in nutrient conditions and one which is not counteracted by succession even as hundreds of feet of serpentine rock are weathered down through thousands of years. It is unreasonable to expect the mature ecosystems or climaxes on the two soils, developing in relation to differing nutrient levels and representing different nutrient economies, to converge. If we regret that serpentine soils will not in time become fertile, our regret may well be tempered by the consideration that their very lack of value will help to save from exploitation these areas of extraordinary interest.

Summary

1. Vegetations of low elevations on serpentine and on quartz diorite were compared with techniques of gradient analyses in the Siskiyou Mountains of southwestern Oregon.

2. The vegetation pattern on diorite is characterized by closed Douglas fir-sclerophyll forests, whereas open, stunted stands of pines and other conifers appear on serpentine. Undergrowth in intermediate stites on serpentine shows an unusual development of a two-phase structure of grass and shrub patches, and in all sites on serpentine numerous endemic herb species occur.

3. Relatively few plant species occur on both diorite and serpentine, and the two floras are shown to be in marked contrast in representation of floristic regions. A means of expressing average range and direction of greater extent for a flora was devised. This shows the serpentine flora to be much more restricted in average extent and to have its greatest extent toward the south, in contrast to the diorite flora.

4. Evidence indicates that Siskiyou serpentine vegetation is climax, although affected by fires.

5. Serpentine vegetations appear in general to be characterized by apparent xeromorphism resulting from basic reduction of productivity, reduction of structure toward the lower strata, and dominance of conifers and especially pines, sclerophyllous shrubs, and grasses. As parts of ecosystems differing fundamentally in nutrient economy, vegetation patterns on serpentine and diorite

differ in almost every respect which can be described or measured.

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NOTES AND COMMENT

A RECORD OF THE EARTHWORM, *SPARGANOPHILUS EISENI*, FROM THE BASIN OF WESTERN LAKE ERIE

Benham (1892) described the genus *Sparganophilus* from specimens collected from among the roots of waterweeds growing on the banks of the Thames River in England. It is generally believed that specimens collected by him and named *S. tamesis* had originally been introduced from North America. Smith (1895) described *S. eiseni* from material collected from the mud sediments in the Illinois River and some bottomland lakes connected with it at Havana, Illinois, where these aquatic earthworms were found to be common. They were most abundant near the shallow margins. The species has been studied in detail by Hague (1923).

In a survey of annelids found in the Great Lakes region, Moore (1906) collected *S. eiseni* on the bottom of Lake St. Clair and reported one small specimen from under a rock at Squaw Bay on South Bass Island in Lake Erie. Olson (1928) mapped the distribution of this species which he collected in Ohio. Collecting sites are given for the shoreline of western Lake Erie. In the records of the Stone Institute of Hydrobiology there are also reports on the collection of this species from shallow water on the shoreline of Cedar Point and of South Bass Island (found in 3 inches of water at Beimiller's Cove, July 10, 1916; four specimens collected in shallow water of beach front at Terwilliger's Pond, Put-in-Bay, in July, 1918). Also, in a manuscript deposited at the Institute (Wright, Stillman, *et al.* "A limnological survey of western Lake Erie with special reference to pollution." p. 672. 1929.) there is a notation that "occasional specimens of an annelid (*Sparganophilus*) were taken in the bottom sled collection."

Heretofore, no records have been published on the collection of *S. eiseni* from the basin of western Lake Erie. In the summer of 1953, three collections were made on class field trips as follows. On June 26, 1953, a specimen was collected from a depth of about 30 feet of water 7.5 miles west of South Bass Island on the edge of Niagara Reef by means of an otter trawl. Two more were collected on July 9, 1953, from a depth of about 32 feet between South Bass Island and Kelley's Island, and another one on July 24, 1953, from a depth of 37 feet some 3 miles east of Middle Island. This species is apparently adapted to living in an aquatic environment of considerable depth and may possibly be introduced into bodies of water from escaped fishing bait.

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CAREX KOBOMUGI AT ISLAND BEACH, NEW JERSEY

The migration of *Carex kobomugi* Ohwi and its successful invasion of the established flora at Island Beach in Ocean County, N. J., took place something over twenty years ago. A collection by C. W. Townsend dated Nov. 1, 1929, is deposited in the Gray Herbarium. No other invasion along the Atlantic coast has been recorded. The real estate at Island Beach, now a state park, was owned by the Barnegat Bay and Beach Company for the estate of Henry Phipps. For permission to enter the property and for many other courtesies, the author is indebted to the late Francis P. Freeman and to Captain Joseph Tilton, resident managers of the property. Names of plants from the area are those recognized by Fernald (1950).

The invasion of an area by plants from the outside is not an unusual phenomenon. Correll (1950) states that "within the past fifteen years six species of orchids have been added to our flora." One of these, *Zeuxine strateumatica* (L.) Schltr., came to Florida from Asia. Ames (1938) has suggested that protocorms of the orchid might have been distributed with stolons of centipede grass which "was introduced in 1917 from regions in China where *Z. strateumatica* is a native, and the length of time since the introduction of the grass to the United States would seem to be commensurate with the length of time it has taken for the orchid to become naturalized." Fernald (1930) has noted that *Carex kobomugi* "comes from the same region (northeastern Asia) as the seashore species, *Artemisia stelleriana* Besser, which has rapidly fixed itself upon our coastal dunes and beaches." But Fernald (1950) also indicates that the *Artemisia* came by invitation and has become naturalized from cultivation.

The late Francis P. Freeman proposed the hypothesis that the colony of *Carex kobomugi* has developed from plants discarded from a passing ship and washed ashore. Large vessels ply offshore, often in full view from this point. The plant could have been pitched onto the fore dunes and heeled in by waves of a storm tide.

The plant must have been almost immediately in competition with established *Ammophila breviligulata* Fern. which covers all the dunes thereabouts. Like *Ammophila*, it is never more healthy and robust than when growing on a fore dune where the sand is most active. Its possible value as a sand binder immediately occurred to Mr. Freeman and he told the writer of several inquiries about it being received from various sources including the Pacific coast where another species, *Carex macrocephala*

Willd., is found in similar locations. Soil Conservation Service work was in progress in Oregon at the time, but their report (1941) does not mention either species.

Our interest in this plant dates from 1939 and since then it has been under observation as part of our studies in the ecology of the New Jersey shore area. In July, 1939, the patch extended 43.0 meters along the dunes and measured 46.3 m. across. This length measurement and all subsequent ones have been made from the farthest plant located at one end to the farthest plant located at the other end of the patch. The measurements have not always followed the same line therefore. At least one fixed point would have been desirable (but fixed points are not easy to establish on sand dunes without disturbing the plant-sand equilibrium, particularly during the early stages). In measuring width, we have selected a line across the dune range where the *Carex* seemed widest in extent. This too has not always been in the same place. The occupation of fore dunes and the destruction of the same and the continued struggle between *Carex* and the shrubs to the rear have been modifying factors. The tabulated data of ten measurements over twelve years, Table I, seems to clearly indicate a continued progress along the dune range and a definite give and take crosswise.

TABLE I. *Extent (meters) of Carex kobomugi stand at Island Beach, New Jersey*

Date	Length	Width
7/26/39	43.0	46.3
10/ 1/42	49.1	45.7
4/14/43	50.0	49.2
5/ 2/44	52.1	48.2
5/ 3/47	52.1	44.2
9/14/48	57.6	52.0
7/26/49	58.2	49.1
7/18/50	57.6	49.4
4/12/51	55.9	49.4
9/16/51	58.5	50.7

No new patches of *Carex kobomugi* have appeared and no seedlings have been found; but who has found seedlings of *Ammopila?* The *Carex* flowers about the end of May. It is dioecious and both plants are present. Staminate and pistillate spikes appear (Fig. 1). By mid-June, the fruits are enlarged and milky. By autumn they appear to be mature. Seeds collected on October 1, 1942, gave every appearance of maturity. Sent to the N. J. State Seed Laboratory, they were given a 74 day test but although some variation of temperature and shock was applied, there was no germination. Propagation, then, at Island Beach, appears to be limited to vegetative extension of the colony through growth of the rhizomes.

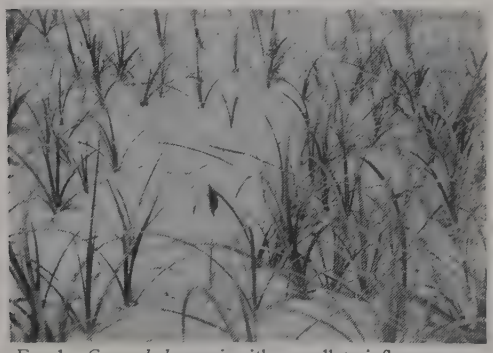

FIG. 1. *Carex kobomugi*, with carpellate inflorescences.

In comparing this plant with *Ammophila*, it has not been practical to dig into the dunes much, so no data are available on the depth of the rhizomes of the two species. From very limited observations, it is indicated that the rhizomes of *C. kobomugi* are placed deeper, have shorter internodes (2.5 cm. compared with 3.1 cm., average on one rhizome), and root more profusely at the nodes than is the case with *A. breviligulata*. The vertical stalks bud and branch, so that at the surface there may be several stalks in a clump. There may be some stooling apparent and also, of course, the shoots may come up at a slight angle and intensitfy the clumping appearance. On July 26, 1939, two quadrats in what appeared to be the densest part of the stand averaged 357 shoots per square meter.

Where sand is moving, it may be difficult to determine the leaves' relationships to the shoots of the partly buried plants. As many as 22 leaves have been found on a shoot. A robust plant may have leaves 45-50 cm. long and about 1 cm. wide, with the typical three-ranked arrangement of a sedge. These leaves arch over, the height of the arch being about 23 cm. above the sand. Nearby *Ammophila* plants have leaves 80-95 cm. long and less pronounced arching (Fig. 2), though one may find circles drawn in the sand around both plants as the wind moves the leaf tips. Both plants protect the dunes throughout the year but there appears to be a tendency of the *Carex* leaves to shred and a greater volume of fibrous remains appears to continue attached to the stem.

FIG. 2. *Carex kobomugi*, with *Ammophila* center foreground and along dune crest.

Anyone who has visited an aggressive stand of *Ammophila* has noted the stems in a straight row of diminishing height toward the growing end of the rhizome. It is difficult to find such orderly advance of *Carex kobomugi* though indications of it have been seen. Such measurements as have been possible on this stand indicate that *Ammophila* may push out 6 m. or more onto the upper storm beach beyond the *Carex*.

An analysis of the stand, made November 24, 1950 is presented in Table II. This analysis is based upon 30 quadrats of 1 sq. m. each, taken at 4 m. intervals across the stand in both directions, always starting with the outermost plant of *Carex*. It will be noted that on only one quadrat was no space (bare sand) visible while at the other extreme, out on a fore dune, as much as 96% space was found. The average of 59.5% space indicates a considerable opportunity for sand movement.

TABLE II. *Composition of Carex kobomugi stand at Island Beach, New Jersey*

Plant	Frequency index	Stems per sq. m.		Cover	
		Average no.	Extremes	Per cent	Extremes
Carex	100	123.3	16 - 291	37.4	2 - 100
Ammophila	90	02.6	0 - 84	6.4	0 - 30
Solidago	73	5.6	0 - 28	5.6	0 - 25
Lathyrus	7	2.5	0 - 3	3.5	0 - 7
Space	99	...	...	59.5	0 - 96

The establishment and continued extension of this colony demonstrates the ability of the *Carex* to compete successfully with *Ammophila* under dune conditions. *Ammophila* is tenacious here as in other plant communities on the offshore bars (Table II), however. The ratio of *Ammophila* is rapidly reduced by the *Carex*. In the first four quadrats (13 m.) the ratios of the stems *Carex*/*Ammophila* were 16/84, 90/80, 142/25 and 133/17. But rarely a square meter can be found without *Ammophila* represented—only 3 out of 30. The other expected dune associates are also present. On the sea side, these include *Cakile edentula* (Bigel.) Hook., *Euphorbia polygonifolia* L., and *Artemisia stelleriana*. On top of the range, one sees *Lathyrus japonicus* var. *glaber* (Ser.) Fern. and *Solidago sempervirens* L. These plants do not seem to be as congenially associated with the *Carex* as with the *Ammophila*. Their erratic occurrence on dunes generally seemed to rule out frequency or density comparisons. The tendency of *Solidago sempervirens* to grow in clumps was noted. In *Carex* stands, leafy stems of *Solidago* appeared singly or in a maximum of six per clump except near the thicket (to be discussed later); in *Ammophila*, just beyond the *Carex* stand, clumps were the rule, with up to 30 stems each. It appeared that height measurements might point up this difference. Sixty stems of *Lathyrus* growing among *Carex* averaged 26.2 cm. tall while an equal number a few meters northward in *Ammophila* averaged 37.8 cm. in length. Fifty stems of *Solidago sempervirens* growing among *Carvex* averaged 16.8 cm. while the same number in an *Ammophila* stand averaged 32.0 cm.

Back of the dune ridge one encounters a thicket zone. The ecotone is fairly sharp and the situation between the two communities may be one of each finding equilibrium with its physical environment as much as it is a stalemate in competition. Wells and Shunk (1938) have pointed out the importance of salt spray in this regard. *Myrica pensylvanica* Loisel. is ordinarily in the forefront of woody plants and it effects sufficient stabilization so that *Rhus radicans* L. and *Parthenocissus quinquefolia* (L.) Planch, can overrun the area. *Carex kobomugi* does not penetrate this plant combination. Instead, the sand moved over the dune ridge into this thicket is followed by *Carex* colonization. This system of dynamics is occasionally accelerated until a segment of the thicket is cut off and isolated.

There is one more test that the *Carex* must meet—its resistance to blowouts and windsweeps. No blowouts have occurred within the dune range though considerable changes have been noted in the frontal aspect and fore dunes. There is a windsweep through the dune range just south of the *Carex* stand. Since 1949 this windsweep has undercut the *Carex* northward slightly, but it has never developed sheer cliffs of sand nor have rhizomes of the plant been exposed to the extent that they have been on the south side of the windsweep under *Ammophila*. The prevailing storm winds are northeasterly though the highest wind velocity may come from any direction in the course of time. This fact may be more important on occasion than the plant cover. Furthermore, different dunes vary widely under *Ammophila* in their resistance to wind. The most that can now be said is that wind work under *Carex* has been slight in three seasons, the extension of the colony northward at least holding its own with the undercutting.

SUMMARY

In something over twenty years, a colony of *Carex kobomugi* has been able to invade and establish itself successfully on the active dunes exposed to the full effect of storm winds and salt spray on a barrier bar some four miles offshore. The absence of seedlings may indicate its inability to complete ecesis. But its successful competition with the plants ordinarily occupying this habitat seems to have been amply demonstrated.

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SIMPLIFIED METHOD FOR THE STUDY OF INTERACTING HOST-PARASITE POPULATIONS

The fundamental factors involved in the interaction of host-parasite populations may be ascertained readily through the use of small organisms in artificial environments, provided that the population generations are distinct and the generation time and power of increase are artificially limited (DeBach and Smith 1941).

An artificial "universe" that appears to be exceptionally suitable for studying interacting host-parasite population was designed by the writer eighteen years ago (Flanders 1935). This universe with its interacting organisms, *Sitotroga cerealella* (Oliv.), the Angoumois grain moth, and its egg parasite *Trichogramma* sp. has certain definite advantages not possessed by any other systems, such as those which include *Musca domestica* L. as host and *Mormoniella vitripennis* (Walk.) as parasite (DeBach and Smith 1941) or *Ephestia kuhniella* Zell. as host and *Idechthis canescens* (Grav.) as parasite (Flanders 1948). Stock cultures of *Sitotroga* and *Trichogramma* are easily and cheaply maintained by using methods similar to those described by the writer (Flanders 1930), but on a much smaller scale.

The Moth-Production Unit

The moth-production unit described here was developed by Dr. A. W. Morrill of Glendale, California.

Pure cultures of *Sitotroga* are maintained on small grains (barley, sorghum, or wheat) held in wire-screen baskets, each of which measures 1 inch in width, 15 inches in length, and 10 inches in depth. The grain is completely infested by placing the filled basket on its side, spraying it lightly with water and then dusting the moistened surfaces with eggs of *Sitotroga*. When the grain thus infested begins to yield adult *Sitotroga*, the baskets are set upright, ⅛ inch apart, in a moth-emergence-and-collection box large enough to hold all the moth-producing grain on hand, regardless of the different ages of the infestations. As each infestation wears out, it is replaced.

The inside surfaces of the moth-emergence box should be smooth and free of minute crevices, except at the one end consisting of a wire frame covered with cloth or burlap and tapering outward for about 10 inches. A screw-cap ring is attached to the wire extension at the tapered end, and into this is screwed a 1-quart glass fruit jar. Since the newly emerged moths tend to alight on the cloth, a quick jerk of the extension causes them to drop into the jar, which is then removed, capped with a 20-mesh wire screen, and inverted over an egg-collection trough.

Complete utilization of the grain by a single moth generation permits such a rapid turnover of stock material that the occurrence of parasites and other grain insects which may interfere with *Sitotroga* production is prevented.

The Experimental Universe

The dimensions of the experimental universe are based on the maximum dispersion in total darkness of more than 10,000 *Trichogramma* adults. This was found to be about 36 inches from the point of release. Consequently, the universe set up measured 18 inches by 18 inches by ¼ inch and provided on its inner surfaces an area of search of about 4½ square feet. In such a universe an active, short-lived parasite such as *Trichogramma* (0.5 mm. in length), individually searching at random for a sessile host (0.5 mm. in length), can cover only a fraction of the area. With hosts evenly distributed over this area, it appears that a parasitism exceeding 80 per cent cannot be obtained with less than one parasite per square foot.

Each universe consisted of two plates of double-strength window glass (18 x 18 inches) held apart by four small corks (each 5/16 inch high) and taped together at the edges by strips of ordinary gummed paper tape, such as is used in sealing packages.

In preparing a universe for each experiment, each plate of glass is placed on graph paper, in order that the host eggs may be uniformly spaced. The eggs are placed on the plate by means of a small camel's-hair brush consisting of only several hairs. The brush is dipped in water, and the eggs are picked up one at a time and transferred to the glass plate. The water softens the material on the surface of the host eggs and this, upon drying, fastens the egg firmly to the place. In the process of developing this work, about 20,000 eggs were thus used. These eggs are comparatively tough and not easily injured. Freshly deposited eggs are used so that they will remain susceptible to attachment for a limited period, or for about 5 days at a temperature of 25° C. The eggs are placed at the edges of only one of the plates, so that when the container is set up all the eggs are practically the same distance apart. After the eggs are in position, the corks are placed near each corner of the bottom plate and the other plate is inverted over it. The gummed tape is then placed around the edges of the universe, holding the plates in place and preventing the parasites from escaping.

Only female parasites reared on *Sitotroga* eggs are used, and these are fed honey before being placed in the units, where they live about 4 days. For minimum variation in results, the parasites should be of the same age in all tests.

The transfer of female parasites from the stock culture to a "universe" is accomplished as follows. Parasitized *Sitotroga* eggs from which *Trichogramma* is due to emerge are placed in a glass vial containing a hair-line streak of honey. This vial is held in darkness until parasite emergence begins. After an hour or two of exposure to light and to a relative humidity of about 60 per cent, the newly emerged *Trichogramma* are anesthetized with carbon dioxide. While thus immobilized, the females are placed in sections of glass tubing (⅛ inch x 1½ inches) from which they are to be discharged into the universe. The number of females placed in a glass tube equals the number to be used in a single universe. When a universe is ready for the parasites, an aperture is made in its paper sides for the insertion of a tube and the release of the parasites. The aperture is then closed with a piece of the paper tape.

Eleven host densities may be used when the *Sitotroga* eggs are evenly spaced 1 to 6 inches apart over the area of the universe. The host populations may then number either 18, 41, 52, 74, 98, 130, 164, 290, 394, 452, or 650 per universe. For each host population the writer has used parasitic populations of 5, 10, and 15 female *Trichogramma*.

The time required to set up a universe ranges from 30 minutes to 2 hours. When completely set up, each unit is placed in a dark room having a temperature ranging between 24° and 26° C., and relative humidities from 60 to 70 per cent. After 6 days these units are removed and

the position of the parasitized and unparasitized eggs is plotted on graph paper. This is done before the units are taken apart to be cleaned and refilled, since the parasitized eggs are readily distinguished because of their black color.

Discussion and Conclusions

The advantages of the *Sitotroga-Trichogramma* experimental universe in studying host-parasite interactions are the following:

The universe is readily cleaned and reconstituted; it is transparent, so that the degree of parasitization is readily recorded, and it is free of organic material that may influence the searching action of the parasites. The host and its parasite are easily placed in the universe at accurately known densities. The number of encounters of host by parasite appears to be directly proportional to host density. Searching by the parasite is random, although the distribution of its progeny per host is not, for it deposits one egg per host at the rate of about three per hour. Since the parasite has a strong tendency to avoid hosts already parasitized (Salt 1936), the mortality of the host through superparasitism is at a minimum. The adult female parasite has no habits, such as host-feeding, that are inimical to successful parasitization.

The "life" of each universe (each artificial generation) is less than 6 days at 25° C. because parasitization (host discovery) is apparent by the coloration of the host 4 days after attack.

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A NOTE ON THE GROUPING OF LATERAL ROOTS

The occurrence of the lateral roots of primary root systems is in a regular pattern which is well-known but of which certain features have been mostly neglected. It is known, for instance, that the primary root systems consists of a primary root with the primary laterals, which are branched or not branched, that may arise on it. But that these groups are regular organs of the root system, and are comparable to the boughs of the shoot, has not been considered. They are, in fact, boughs of the root, or root-boughs, the character of which largely defines that of the root system of which they are a part.

Root-boughs vary greatly in their character. Some are very large, others are very small. They vary in branching, and in length of life; some also are herbaceous, others are woody.

In this note, however, consideration is given chiefly to the order of branching as it is related to (a) the type of root-bough, and to (b) its environment. Of the last mentioned, it may be suggested that in soil with high water content, the ultimate order is low, where the soil is with little water, it is high, and in relatively dry, or relatively moist soil, it is also intermediate.[1]

The lateral roots branch to (a) the "highest" order, or to (b) the "ultimate" order. The former is related to sub-optimal environmental features, such as too low temperature; it is, consequently, a variable feature. The "ultimate" order, on the other hand, is a specific feature which is largely dependent on optimal conditions of growth; it is a fixed character. The maximum ultimate order known is the 5th.

Root-Boughs of Herbaceous Plants

Root-boughs of vegetables[2]

The researches on the roots of cultivated plants to be referred to were conducted in eastern Nebraska. The cultures were in fertile, dark-brown, Carrington silt loam, in excellent conditions of tilth. It was penetrable by roots for several meters. A good supply of moisture to root depth was present throughout the entire growing season.

The leading results given here will include: (1) the highest order of branches, (2) the plant in reference with (3) the reference figure cited in parenthesis.

The highest order formed was the 3rd or the 4th. Of the two, the 3rd order is apparently the better established.

The 3rd-order lateral was the highest found in the following, *viz:* carrot (63), eggplant (77), okra (60), parsnip (67), pea (52), pepper (80), rutabaga (44), and squash (88).

The 4th-order lateral was the highest order of the following, *viz:* bean (58), cabbage (29), cucumber (82), muskmelon (85), tomato (73), and turnip (42).

In all instances the root-bough as an organ of the primary root system is distinctly marked.

Root-boughs of wild annuals[3]

In southern Arizona, the winter-active annuals and those that are active in summer occupy the same habitats. These are mostly the mesa, the flood-plains of washes and streams, and the slopes of hills. Where the slopes and mesas join, the soil is relatively deep and with a favorable water supply.

In southern Arizona, the cold season is with rain. In spring, the rains decrease and finally cease, but with the coming of the hot season they return. A second dry period is in late summer-early autumn. The four well-defined seasons are in most, if not in all annuals, the boundaries of the activities of their root systems.

Although the roots of the plants active in both rainy seasons have been examined, only those of summer will be referred to in this summary. The highest orders of

[1] A close relation lies between the root-bough and the absorption of water in that the absorbing laterals are wholly, or in part, of the ultimate, or the highest order.

[2] Based on Weaver and Bruner (1927).

[3] Based on Cannon (1911).

the lateral roots developed concidentally with the summer rains are the 3rd and the 4th.

Among the species with 3rd-order laterals, with page references in parentheses, are the following, *viz: Anoda thurberi* (26), *Datura* sp. (27), *Ditaxis humilis* (27), *Dysoda papposa* (28), *Pectis prostrata* (29), and *Solanum elaeagnifolium* (29).

The highest order is the 4th in the following: *Amaranthus palmeri* (26), *Aster tanacetifolius* (26), and *Cladothrix lanuginosa* (27).

It is evident, therefore, that the highest orders of laterals, which may be the ultimate orders, are comparable to those of vegetables, *q.v.*

Root-Boughs of Trees

As was shown above, the root-boughs of annuals are small and can be excavated with relatively little difficulty. Moreover they develop to maturity in one season. But the root-boughs of trees, on the other hand, may be many meters in extent, and their lifespan may be without evident limitation. It is known, however, that in trees, development may be in stages which are, generally speaking, three—the seedling, the sapling stage, and that of the mature tree. These relate both to the shoot and to the root system, and, as will be shown below, they concern also the root-boughs, which when young are small and can be completely excavated. Finally, the results of such research can be directly applied to the old tree, and especially to the old root-boughs.

Root-boughs of seedling trees[4]

The seedling trees to be considered in this section were grown in southeastern Nebraska in locations where the species may naturally occur. Of these one is a north-facing scope where *Tilia americana* grows; a second is a southwest slope with *Quercus macrocarpa;* and the third is a hill crest which is under cultivation. Among the effective environmental factors, the soil varies from clay to alluvial soil and to loess. The light also ranges greatly in its intensity; there is full insolation on the hill and heavy shade on lower ground. The greatest growth was on the hill (prairie), the least was in the *Tilia* forest.

The cultures continued to and through the third year. The following are among the most striking observations and results. During the first year, all seedlings showed root growth in each of the three habitats and the same was true the second season; the highest orders each year were the 2nd and 3rd. But the third year on the prairie, all seedlings were with 3rd-order laterals; in the oak forest two of three had 2nd-order, and one 3rd-order laterals; and in the *Tilia* forest, only the roots of *Tilia* showed growth—it formed laterals of the 2nd order the 3rd year.

In the prairie habitat, therefore, there is the third season a coincidence between the order of branching and the age of the seedlings. There may be a similar relationship in seedlings of the fourth and fifth years, as is suggested in young sapling trees (see below), but in yet older trees such relationship appears not to hold.

Root-boughs of sapling trees[5]

The root systems of sapling trees were investigated near Fayette, Missouri. Of the species observed, and their habitats, *Acer negundo* is on the flood-plain; *Juglans nigra* and *Gleditsia tricanthos* grow on the flood-plain and the fertile upland; *Acer saccharum, Carya ovata,* and *Quercus rubra* occur on the moist, well-drained slopes; *Quercus macrocarpa* inhabits upland clay; and *Populus sargentii* is on loam soil and clay.

[4] Based on Holch (1931). The orders of branching were determined mostly by the writer from text figures.
[5] Based on Biswell (1935).

The sapling trees of these species (of which the youngest are evidently of the seedling stage) were from 3 to 16 years old. Their age and the highest order of laterals they formed (with the figures referred to in parentheses), are given in the following table.

	Orders of laterals	*Age, years*
Populus sargentii	4 (14)	3
Quercus rubra	5 (10)	5
Gleditsia triacanthos	4 (3)	6
Juglans nigra	5 (9)	7
Carya ovata	5 (11)	8
Quercus macrocarpa	5 (13)	8
Acer negundo	5 (6)	15
A. saccharum	5 (12)	16

It appears, therefore, that regardless of the age, the highest order of laterals formed is the 4th or the 5th, and, accordingly, the types of root-boughs are I-V. However, some species may develop specialized laterals, such as rope root and sinkers, in the sapling stage. These may be the 2nd, or other order, giving to the root-bough an additional type, type VI (see diagram, root-boughs of the old oak tree, below.)

Root-boughs of an old oak tree: Quercus macrocarpa[6]

In eastern Nebraska where the root system of the old oak was studied, the species is a forest tree. The soil of the habitat is fine sand, silt, and clay with the clay predominating below 32 cm.

The root system is extensive and relatively superficial. The tree which was mostly studied was 11.45 m. high. It had a basal stem diameter of 35.5 cm. and was 65 years of age.

The following is a summary of the most prominent features of the root system:

1. Fifteen large primary laterals arose on the first 38 cm., and seven others between 38 and 90 cm., on the primary root. The superficial portion of the root system consisted, therefore, of about 22 root-boughs.

Most of the 1st-order laterals were 6 to 18 m. long before turning downward; this is the length of the superficial portion of these root-boughs.

2. Many 2nd-order laterals (sinkers) grew vertically downward 2.2 to 4.5 m.; others extended obliquely or directly upward; and others of the same order (rope roots) reached outward about 16 m. About one-fifth of the 2nd-order laterals were sinkers.

3. The laterals of the 3rd order were in large numbers; so many as 28, for example, arose on the basal 1.2 m. of one sinker; some branches of the order ran obliquely outward from 3, to more than 4 m.; all were relatively long.

4. The 1st, 2nd, and 3rd-order laterals comprise the framework of the root-bough and define its extent.

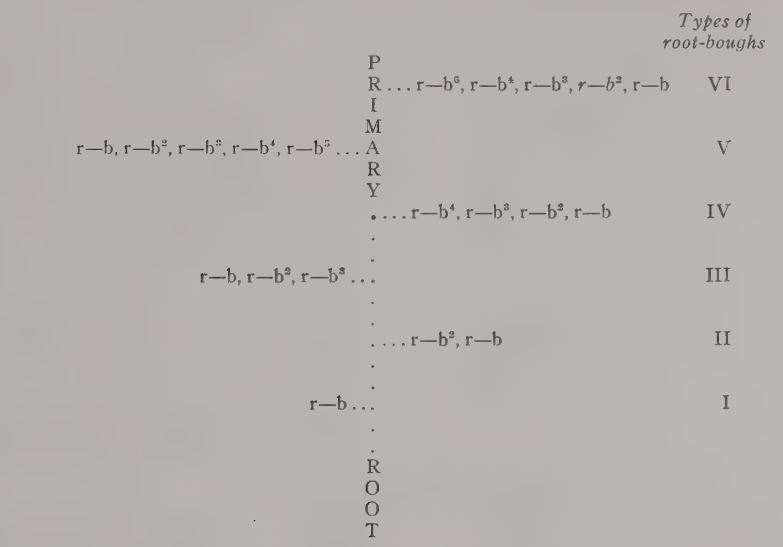
5. Branches of the 4th order were short and were present in abundance.

6. The 4th-order branches were clothed with masses of laterals of the 5th order which is the ultimate order of laterals of the oak.

7. Root-boughs of types I-V are of conventional kinds, as those of seedling trees, but VI-root-boughs are, as in sapling trees, special laterals of orders previously formed, mostly of the 2nd order. Of these, sinkers and rope roots are prominent features of the old root system of the oak.

[6] Based on Weaver and Kramer (1932).

ROOT-BOUGHS OF THE OLD OAK: QUERCUS MACROCARPA
Composition and relative position of root-boughs (r-b)



In the above diagram, which is generally applicable in primary root systems, the relationship of the root-boughs to the root system is suggested. Both the root-boughs and their branches arise distally and mature proximally and are formed consecutively.

Types I to V are of the seedling stage of the oak tree; type VI is of the sapling stage and becomes a dominant (?) factor in the old root system.

SUMMARY

1. In primary root systems, the primary lateral roots branch to form groups of lateral roots which are analogous to the groups of branches, and which form the boughs of the shoot; they are root-boughs, occurring in all primary root systems.

2. Root-boughs are simple if they do not branch, but compound if branches are formed.

3. Compound root-boughs are branched to the 2nd, 3rd, 4th, or 5th order; the 5th is the highest order now recognized.

4. The highest order of laterals a plant can develop is the ultimate order. Based on the ultimate order, there are five classes of root-boughs, as follows: type I, unbranched; type II, branched to the 2nd order; type III, branched to the 3rd order; type IV, branched to the 4th order; type V, branched to the 5th order. (In addition is type VI, which is type V with specialized laterals.)

5. The types are tentatively classed ecologically as follows: type I are aquatic; type II are hydrophytic; type III and type IV are mesophytic; type V are xerophytic.

6. All types of root-boughs which are characteristic of the species are present at the same time.

7. The highest order of laterals in vegetables, which may be the ultimate order, is the 3rd or the 4th.

8. The highest order of laterals developed by winter-active annuals of southern Arizona, is mostly the 2nd; the highest of summer-active annuals is the 3rd or the 4th. In these wild annuals, the highest may be the ultimate order.

9. Young trees of the seedling stage, three years of age, may be branched to the 3rd order when growing under favorable conditions, as, on the prairie; in the *Tilia* forest, only *Tilia* seedlings show growth.

10. The seedling stage may end with the formation of the ultimate order of laterals which is the 5th order, or less.

11. The sapling stage follows the seedling stage and may be characterized by the formation of specialized lateral roots of orders in being (as in *Quercus macrocarpa*).

12. In trees, the sapling stage appears not to have a distinct ending, or the mature stage a distinct beginning. The ultimate order of the laterals is the same in both; where specialized laterals are present, as in *Quercus macrocarpa*, they may comprise a large proportion of the root-bough of the old tree.

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INTRODUCTIONS OF AMERICAN CRAWFISHES INTO FOREIGN LANDS

At least two species of American crawfishes which have been introduced into foreign lands have found habitats well suited for their survival and spread. One of these, *Orconectes limosus* (Rafinesque), was imported into Europe at the end of the last century following an epidemic disease which decimated the population of native crawfishes. From its introduction in 1890 in the vicinity of Frankfurt in Brandenburg, Germany in the Meitzel River (a tributary of the Oder), and in 1894 in the vicinity of Fécamp on the north coast of France, it has spread, largely through the extensive canal systems, to the Oder, Weichsel, Elbe, Havel, Main and Seine rivers of the North Sea drainage, the Loire and Charente rivers of the Atlantic drainage, and the Saone River of the Mediterranean drainage (Bott 1950, Vivier 1951). In the rivers of France and Germany, *O. limosus* has proven to be of value (for human food) or of no particular economic importance (André and Lamy 1935).

The second, *Procambarus clarkii* (Girard), has been introduced into two countries greatly removed from its normal range and into three areas within the United States, also outside of its normal range. The presence of this species in a stream near Pasadena, Los Angeles County, California was long ago recorded by Holmes (1924), and its supposed introduction into Las Vegas Wash in southern Nevada has been discussed by Hobbs and Zinn (1948). In California, it is also known to have been introduced with success in Sonoma County in the vicinity of Santa Rosa (Hobbs and Zinn *loc. cit.*) and in Santa Barbara County in the vicinity of Santa Barbara. The source of the original stock in these cases and whether the introductions were natural or by human agency (either accidental or purposeful) remains unknown. Both Holmes and Hobbs and Zinn suggested that natural introduction by normal migration is highly improbable. Recently in a letter, Mr. Thomas K. Marbury informed me that he had released 100 pounds (estimated at between 700 and 900 individuals) of *P. clarkii* into ponds on his "crawfish farm" near Hudson, Pasco County, Florida, in 1951. It is almost certain that escapes from this introduction will occur. Whether this species will be able to survive in southern Florida is problematic although its favored habitat is abundant. Hobbs (1942) recorded *Procambarus alleni* and *P. fallax* from Pasco County; it is conceivable that *P. clarkii* may not be able to compete with these two species, both of which prosper in the same type of habitat.

It is suggested that the presence of *P. clarkii* in California and Nevada stems from several accidental introductions as suggested here as the probable outcome of the Florida experiments by Mr. Marbury.

Through the courtesy of Dr. Masuzo Ueno, Director of the Otsu Hydrobiological Station at Otsu-shi, Shigaken, Japan, and Mr. Alan Thistle, Director of the Division of Entomology and Marketing, Board of Commissioners of Agriculture and Forestry at Honolulu, the details of the introductions of *P. clarkii* into Japan and the Territory of Hawaii respectively are here published for the first time.

In 1930, Mr. Yoshinosuke Kono obtained 100 Louisiana specimens from Mr. Percy Viosca, Jr., in New Orleans to take to Japan. There the crawfishes were desired for propagation as food for American bullfoods, *Rana catesbeiana* Shaw, which had been introduced into Japan in 1918. Only twenty of the crawfish survived trans-Pacific shipment and were used to stock the Iwase Frog Farm at the town of Ofuna, near Tokyo. Escaped individuals thrived in the ditches and rice fields around the town of Ofuna and then spread to the swampy areas in the suburbs of Tokyo. From here they spread westward on Honshu, the main island of Japan. During the past twenty years, *P. clarkii* has become firmly established in the western half (southern part), chiefly on the Pacific side of the Japanese islands, taking readily to the ever-present ditches and rice fields. Kubo (1947) recorded this species from the Kwanto district only. Dr. Ueno writes that they are extremely troublesome to the farmers because of their burrows in the rice fields and in cutting off the young rice shoots on which they feed. In the suburbs of the city of Osaka, especially, this crawfish has been noted as a severe pest since 1948. Ueno estimates its abundance in rice fields as from 12,500 to 110,900 per hectare [calculated at the rate of 1,200 kilograms (= 2,645 pounds) per hectare].

In 1934, Mr. C. P. Holmes of Honolulu imported eight tubs (about 400 specimens) of *P. clarkii* from the Feather Hill Ranch, Santa Barbara, California in connection with the establishment of a frog farm on Oahu. Escaped individuals are reported to be thriving in taro (*Colocasia esculenta*) fields which are flooded. Mr. Thistle writes that in these fields the crawfish interferes with production by burrowing in the embankments and ditch banks and to some extent feeding on the roots and corms of the taro. It has become quite common on Oahu and has been carried also to a few localities on the islands of Hawaii, Kauai, and Maui. On Kauai, it has become established in the Puu Lua Reservoir at an elevation of 3,250 feet, although this colony is reported as still quite small.

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REVIEWS

Two Reviews of Odum's Fundamentals of Ecology[1]

A New Ecology Text Book

In the early part of this century the criticism that was leveled at the study of ecology and the text books written for use in ecology courses was at the constant inclusion of a great mass of new terminology and subsequent confusion in interpretation. This is probably to be expected when new and dynamic subject material is assembled during its first years of development. A few text books on ecology for beginning courses continue to overwhelm the student with this chaotic confusion of terms and concepts, and with a tremendous bulk of material. Dr. Odum in this new book the *Fundamentals of Ecology* has successfully marshaled the rudiments of ecological knowledge into a well organized, readable, basic text.

The text itself is organized into three parts. The first of these is the longest and most complete portion and deals with the fundamental principles and concepts. The ecosystem and the biochemical cycle, limiting factors, energy systems, populations and community organization are principles that are ably developed. In every chapter each new concept is introduced with a terse, clear statement. This is followed by a longer explanation which carefully amplifies the preceding statement. Finally, in completing each section, outstanding dynamic examples of this concept are given. This type of brief and concise presentation should encourage rather than confuse the beginning student.

The chapter pertaining to energy in ecological systems is an excellent example of the treatment given ecological concepts throughout the text. In writing of the ecological pyramids, Dr. Odum shows dramatically in text and figures, the various methods of measuring energy transmission through the various trophic levels. This presentation is simple and straightforward and most fascinating to read.

The second part of the text approaches ecology from the view point of the habitat. The coverage here is of necessity brief, but in most cases fairly adequate. As a botanist, it is my opinion that the treatment given the terrestrial plant communities should be expanded; while the treatment is accurate, it is hardly adequate. The sections on fresh water and marine ecology are especially well written. The illustrative material used in these sections is particularly well chosen. It should be recognized that in a general treatment of habitats needed in a work of this kind, it is impossible to give complete coverage. In order to correct this deficiency the student is referred to studies made of these habitats, published elsewhere. Thus those desiring further information will readily find the sources.

The third part is devoted to applied ecology. The application of ecological principles and concepts in such practical fields as Agriculture, Forestry, Wildlife Management, Conservation, Land Use, Stream Pollution and Human Ecology is a necessary conclusion to any modern text on ecology.

In planning the course of study an instructor can choose to start with Part I or Part II. This is possible because of the complete cross reference system used in the text guiding the reader to other sections of the book where the same material is presented from another viewpoint. This feature certainly gives the instructor using the text a choice of approaches.

This is a well-written text book, finely illustrated, with ample bibliography. It should not only prove useful in the classroom, but will prove helpful as a reference for workers in the field of pure and applied ecology.

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[1] Odum, Eugene P. 1953. Fundamentals of Ecology, xii + 384 pp., 119 figs. Philadelphia: W. B. Saunders Company. $6.50.

Ecology—an Initiation

Publication of a textbook of general ecology designed quite specifically for undergraduates is in itself a significant event, based on at least two presumptions. There must be a sufficient number of courses taught at this level to create the demand, and the science needs to have become crystallized to the extent that a major amount of information exists which can be generalized in terms comprehensible to the student. Few ecologists would entertain much doubt about the first of these assumptions; the author ably demonstrates the truth of the second. The possible influence of the book on the field is substantial, since it should speed the gradual transition of emphasis in field courses from study of interesting isolated bits of knowledge to a more organized investigation with a decided ecological slant.

This is a prepossessing book. Format, paper, typescript and lucid illustrative material combine to make a favorable first impression. Moreover, a closer look reveals that the author has succeeded in his general objective, and specifically presents the more difficult ecological concepts in such a way that they should not be beyond the understanding of the interested undergraduate.

Of the three major divisions, dealing respectively with general principles, habitat, and applied ecology, the first occupies almost two thirds of the book. Particularly in this section, the book, as stated in the author's preface, profits from the recent treatise by Allee, Emerson, Park, Park and Schmidt (1949) in organization as well as in material. An early chapter on ecosystems lends perspective to what is to follow: a brief but adequate discussion of limiting factors, and more thorough treatment of energy relations, the properties of species and mixed-species populations, and of communities. To give some indication of the distinctly modern flavor of the book, sampling of a single chapter, that on species populations, may suffice. Here we find succinct explanations of growth rate, natality, mortality and dispersal, and in addition brief discussion of the life table and the true or intrinsic rate of natural increase. An examination of growth form leads to the most familiar mathematical model, the logistic curve,

and to a fairly critical review of some well-documented population cycles. The chapter closes with a section on dispersion, introducing such concepts as aggregation and territoriality, and pointing out that technical difficulties in the sampling of populations arise largely because of such non-random distribution.

The second major division discusses within the compass of a hundred pages the major habitats: fresh-water, marine and terrestrial, and their characteristic animal and plant communities. While this section may seem sketchy at first, one is amazed at the breadth it manages to achieve in such a circumscribed space. Applied aspects, such as wildlife management or public health are discussed specifically at the end, although examples from practical fields occur throughout the book. A final chapter entitled "Applications: Human Society" rather neatly states the problem without taking sides in the controversy.

It is, of course, axiomatic that a book of this sort must contain some over-simplification and that it cannot be all-inclusive. To the reviewer, viewing the book as a whole, the balance achieved is notable. Furthermore, new terms are clearly defined, and while the author does not believe in "calling a spade a geotome," he does not shrink from useful technical terminology. The index, which is meant to serve as a glossary, is invaluable in this respect. There is an adequate and unobtrusive citing of evidence, much of it quite recent; a few classic studies are also mentioned. The figures and table are carefully chosen and prepared so that they can readily be understood.

Although the shortcuts in presentation do not cause gross misconceptions, a number of concepts are stated more categorically than the evidence warrants. Likewise, while the ideas usually emerge clearly, one does occasionally come across an ambiguous or misleading statement. Thus in a section dealing with mutualism, cooperation and commensalism (p. 178), the author says without documentation or explanation: "Like a balanced equation, it seems reasonable to assume that negative and positive relations between populations eventually tend to balance one another if the ecosystem is to achieve stability." Again, in the discussion of the logistic curve, the reader may well get the erroneous impression that the constants from which the curves are fitted have usually been obtained from data other than those of the growth form curves themselves. At another level, use of the same mathematical notation both for growth and birth rates may cause confusion despite the author's careful cautioning.

With respect to content and emphasis, the reviewer, with minor reservations, is in enthusiastic agreement with the author. Surely the most general section, on principles, deserves to occupy the major portion of the book, with the more specific and applied aspects relegated to a secondary rôle. It is true that description of techniques must be largely omitted in such a presentation, but this, after all, is not a treatise to be used mainly by the research worker. The only basic criticism of content that occurs to the reviewer is that the relation between ecology and evolution is slighted. More explicit discussion of evolutionary implications would provide additional coherence to many of the principles stressed. While there may not be justification for the inclusion of a special chapter on this subject, treatment of population growth form, interspecific competition or endemism in Lake Baikal, for instance, would profit by some discussion of evolutionary results or causes. A minor, but related point to which the reviewer is sensitive is the omission of an account of the cave habitat. Surely, if springs deserve two pages, caves rate at least one.

In preparing a book for the college student, the author has chosen a style which emphasizes the common touch. Certain parts show a profligacy in the use of quotes and exclamation points to stress the personal familiarity of the material to the student. This is one of the reviewer's idiosyncrasies! The student certainly should find the subject fascinating enough without such devices. Moreover, the use of colloquialisms is at times a bit pedestrian, as in the following (p. 232): ". . . there is 'more than one way to skin a cat,' i.e. there is more than one way to accomplish the same ultimate objective," and leads to at least one statement that should provide amusement for the literal-minded, when the author, in a discussion of parasitic food chains (p. 77), speaks of ". . . our friend, the second law of thermodynamics." Such matters are, however, not of major import; possibly students do like this sort of thing.

That the book will find a wide reception seems clear. At last the search of the teacher in this field for a usable text can come to an end. It is to the author's credit that he has not only filled this distinct need, but has set a high standard which future texts will have to face.

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Insect Physiology[1]

There are few environments, save the sea and large lakes, in which numerous species of insects have not successfully established themselves. The impact of the environment has resulted, therefore, in the extreme development of certain basic physiological functions among various insect species. The physiologist interested in muscle physiology discovers that insects have developed flight muscles which may contract 1000 times per second, many times faster than the muscles of other animals. The cytochemist seeking to understand the function of intracellular organelles discovers that insect flight muscles contain giant mitochondria, many times larger than those found in the cells of other organisms. The ecologist studying water metabolism finds that insects cannot only withstand prolonged and extreme desiccation without sacrificing activity, but they can actually gain body water from moderately moist air. The biochemist discovers that, next to the bacteria, insects enjoy a wider range of food stuffs than any other organisms. The embryologist and experimental morphologist select the insect as the animal of choice for a large variety of studies of developmental phenomena. The student of animal behavior finds insects rewarding and amenable subjects for observation and experimentation.

A diverse scientific audience will therefore rejoice in the publication of this authoritative and important book on insect physiology. The aim of the book, in the words of its editor, Professor Kenneth D. Roeder of Tufts College, is "to summarize and evaluate the major trends in experimental research on insects" and to present "a critical discussion rather than a complete review of insect physiology." To this end Roeder has assembled fifteen

[1] Roeder, K. D. (Editor) 1953. Insect Physiology. xiv + 1100 pp., 257 figs. New York: J. Wiley. $15.00.

authorities on various aspects of insect physiology to discuss those papers they consider pertinent and to express their own individual views and conclusions. The choice of authors and the scholarship and diligence of the editor make this volume a significant contribution to the literature of comparative physiology.

The book is well-documented with a bibliography of about 2700 references, approximately one-third of which are to papers published after 1945. Happily, most of the the authors do not withhold their judgment concerning good and bad in the diverse and frequently contradictory literature of this field. Many sections include important ideas and information not previously in print. The 32 chapters group themselves under the following general headings: integument (55 pages); respiration (92 pages); blood and related tissues (126 pages); nutrition, digestion and excretion (131 pages); nervous activity and sensory reception (121 pages); flight and other muscular activity (98 pages); behavior (124 pages); and developmental physiology (153 pages). Subjects like intermediary metabolism which relate to various aspects of physiology are discussed in several places. However, this proves no handicap, for there is a detailed 60-page index.

A. Glenn Richards introduces the subject with a lucid summary of the structure and function of the integument, including changes that occur during moulting, and the physical and chemical properties of the cuticle and its derivatives. Of particular interest to the ecologist is the discussion of the penetration of various substances, notably water, through the cuticle.

The chapters by George A. Edwards on respiratory metabolism include a brief description of the principle respiratory adaptations found in insects, a comparison of the metabolism of hemi- and holometabolic insects, discussions of the effects on respiration of temperature, humidity, oxygen tension, radiation and various chemicals and a brief consideration of diurnal and seasonal changes in respiratory metabolism.

John B. Buck's chapter on the blood is perhaps the most critical and detailed summary of this subject ever to appear. Extensive data, concisely tabulated, are evaluated with due regard to errors inherent in the various methods of blood-analysis. Buck's chapter on the regulation of the internal environment features a stimulating discussion of water conservation mechanisms in terrestrial insects and of osmoregulation in aquatic insects. He concludes: "insects seem to regulate their internal milieu in much the same way as mammals, if not perhaps within quite so narrow limits. If there is a distinction between the two groups it is rather in the greater ability of insects to endure accidental or forced changes."

Especially complete is the section by Max. F. Day and Douglas F. Waterhouse on the structure and function of the gut and the mechanism of digestion. It includes a stimulating discussion of the absorption of water, nutrients and various chemical substances. William Trager examines insect nutrition within the framework of animal nutrition in general, and considers also the nutritional peculiarities of special groups of insects, the role of nutrition in polymorphism and the importance of microorganisms.

The chapters on the nervous system and sensory reception by Roeder and V. G. Dethier are outstanding. They summarize clearly most of what we know about these subjects, and add new and important unpublished data. Even the uninitiated can read these chapters with understanding, for Professor Roeder has furnished the necessary background.

A signal contribution to physiology is Leigh E. Chadwick's discussion of insect flight, which brings together for the first time the manifold problems involved in analyzing this most spectacular of all insect attributes. Beginning with the necessary anatomical description of the thorax and flight muscles Chadwick outlines the factors affecting wing-beat frequency and amplitude, discusses the aerodynamic and metabolic aspects of insect flight, and concludes with an analysis of the neuromuscular mechanisms underlying the exceedingly rapid wing movements.

The chapters on behavior by T. C. Schnierla contain an impressive and valuable summary of the literature. However, the author's involved terminology and round-about prose occasionally obscure the information and the point he is trying to make. Consider, for example, one section heading: "Behavior patterns and effective environment mutually determinative." Consider also the following quotation: "In the analysis of significant correlations of organic functions in behavior, not only their individual contributions to total activity but also their composite organization in it require demonstration. When such evidence is considered together with unifying and organizing processes in the individual as related to the ontogenetic background and to environment, progress is made toward an adequate theory of behavior." This reviewer does not yet understand, quite, what is meant here, but these sentences apparently outline the author's basic viewpoint, which colors the important material he discusses. For the expert, these chapters will doubtless prove valuable, but without a substantial background in the study of behavior they may remain obscure.

In his chapters on embryonic and post-embryonic development and regeneration, Dietrich Bodenstein discusses several examples in great detail, to illustrate certain main principles, and consequently has been obliged to omit a large amount of material. Although we are thus regrettably deprived of Bodenstein's critical appraisal of many subjects, it is gratifying that the basic facts of the developmental physiology of insects are fully covered. Of especial interest to the embryologist, these chapters may introduce the advantages that insect material provides for the study of certain embryological problems.

Bodenstein concludes with a rather complete chapter on the role of hormones in molting and metamorphosis. It is perhaps unfortunate that he chose to discuss insect endocrines chronologically. Thus on page 880 we are told: "the development of *Rhodnius* is controlled mainly through the actions and interactions of two hormones. . . . The brain furnishes the . . . growth and differentiation hormone, and the corpus allatum the juvenile . . . hormone." While on page 909 we are informed that in *Rhodnius* recent experiments show that the growth and differentiation hormone is not secreted by the brain after all, but is secreted by another endocrine organ, the prothoracic glands. Notwithstanding the shortcomings of the historical approach, the material is presented in a stimulating manner and serves as a clear introduction for the general reader.

In addition to the aforementioned subjects, there are chapters on excretion (R. L. Patton), circulation (R. L. Beard), blood cells and fat body (S. C. Munson) and muscle biochemistry (D'arcy Gilmour).

Surprisingly, there is virtually no overlap in these many chapters, a credit to the editor. Moreover, the contents of the present volume do not conspicuously overlap V. B. Wigglesworth's standard "Principles of Insect Physiology." Indeed, the two books complement each other and can profitably be used together.

Several features stand out in this comprehensive book. One is the broad interpretation of their subjects by the authors. In the section on the alimentary canal one finds

such subheadings as "Mechanism of Hunger," and "Frequency of Feeding," subjects about which it is difficult to find information elsewhere. Another useful feature is the information given on the mode of action of enzyme inhibitors, drugs and other chemical agents. Also gratifying, to this reviewer, are the brief and critical discussions of the special methods employed in insect physiology, discussions which will doubtless be stimulating to workers in other fields of physiology. Comparisons with vertebrate physiology and with the physiology of other groups are made frequently, so that the comparative physiologist will find much useful information. For the worker in insect physiology and applied entomology, the book is invaluable and includes such practical information as a tabulation of different insect Ringer solutions. The ecologist, particularly if he is concerned with invertebrates, will find it a storehouse of important material. The book can confidently be recommended to investigators and teachers in all fields pertaining to the biology of insects.

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Fresh-Water Invetebrates[1]

Our knowledge of the invertebrate fauna of the United States has increased rapidly during the past twenty years, but until now there has been no successful attempt to bring together in a single treatise the pertinent information on this large and diversified group. The necessity of consulting scattered references in numerous monographs, journals and obscure publications in order to become familiar with the biology and taxonomy of the common invertebrates has greatly deterred the beginning zoology student from developing a serious interest in the group, and has created major inconveniences for the professional zoologist. These difficulties have been greatly alleviated by this book on the Freshwater Invertebrates of the United States in which the author has admirably handled what to many individuals would be an impossible assignment. He has brought together in a relatively compact book an authoritative treatment of the biology and taxonomy of the free-living freshwater invertebrates of this country, including the insects.

The role as author, according to the preface "has been one of arrangement, organization and selection from a very large mass of published information" rather than supplying original material from his own researches. In this role he chose to emphasize the natural history, ecology and taxonomy, placing secondary emphasis on anatomy and physiology. In general the book impresses one as an achievement in organization and consistency in purpose. Pertinent facts are presented clearly and concisely and details are used sparingly *but* judiciously. Because of a simple and direct, yet thorough, method of treatment of the subject matter the book may well serve as a text for upper classmen and graduate students as well as a reference for the professional zoologists. An impressive roster of specialists who aided in the technical aspects of the various taxonomic groups lends much to the authoritative atmosphere of the entire book.

The ecological tenor of the book is set forth in the introductory chapter by a discussion of the origin of the freshwater fauna, freshwater emigrants to the sea, some major distinctions between freshwater and marine invertebrates, atypical freshwater habitats, dispersal and barriers, and food webs. This is followed by 36 chapters (pages 20-726) each concerned with the general biology and taxonomy of a group ranging from phylum to order. The classification used for all groups incorporates recent changes of major importance. In instances where the taxonomic relationships within a group are not agreed upon by specialists, the author has stated the source of the classification selected. At the end of each chapter is a selected bibliography listing monographic works both in the United States and Europe and pertinent references on taxonomy and general biology.

Two appendices are included. Appendix A. "Field and Laboratory Apparatus" presents photographs of selected pieces of equipment useful in collecting invertebrates and a brief description of their use. Appendix B. contains a list of reagents and solutions and a description of procedures which he recommends for the anesthetization, preservation, fixation and general preparations of invertebrate materials. These appendices will be of particular interest to the beginning student. The index includes names of genera, subgenera, species and subspecies and is carefully done.

Each taxonomic group treated is assigned a chapter heading. In discussing the group, information is presented on general characteristics, locomotion, feeding, reproduction, ecology, geographical distribution, collecting, preservations, taxonomy and information distinctive to the group. The biology of the insects is treated less thoroughly than the other invertebrates and this is understandable in the light of available information of this much studied group. One of the major contributions of the book is the excellently arranged and concisely worded keys for identification of invertebrates to genus and in some instances to species. These keys are compilations and modifications taken from numerous sources, but in most instances closely follow those of widely recognized authorities. The keys are supplemented with pertinent information of geographical distribution, when available, and numerous photographs and line drawings. The latter although numerous are well arranged and illustrate many of the taxonomic characters used in the keys.

Any attempt, especially by an individual, to cover in one volume as broad a subject as the one included in this book will be confronted inevitably with criticism of incompleteness and inaccuracy. Taxonomists no doubt will find it difficult to accept the classifications in their entirety, and some zoologists will object to the dropping of such generic names as *Corethra* and *Chironomus*. Typographical errors occur throughout the book but none that would result in misinterpretation by the reader. In the opinion of the reviewer a criticism of more serious nature is the author's attempt to simplify this large mass of information and to present it in a readable form, and in so doing making statements which represent half-truths. For the experienced biologist this is of minor consequence, but for the beginning student it may be otherwise. A few examples will suffice to illustrate the point at issue.

On page 422 in a discussion of *Mysis* the following statement is made. "Reproduction is restricted to the colder months, and females are gravid between October and May, although a few gravid specimens may sometimes be found as late as June." This represents reproductive conditions in some lakes but most certainly not in all. In a study of *Mysis* in North German Lakes Thienemann found that reproduction occurred only during

[1] Pennak, R. W. 1953. Fresh-water invertebrates of the United States. ix + 769 pp., 470 illus. New York: Ronald Press. $14.00.

the winter months in Lake Voettern while in some other lakes it occurred both in summer and winter. In Cayuga Lake, N. Y. gravid females occur primarily from June to October, but some may be collected in early spring.

In a brief description of the daily vertical migrations of *Mysis* (page 423) the author states, "Populations are confined to the meter of water just above the bottom during the middle of the day, and no amount of sampling above that depth will take specimens." Generally the sexually mature individuals do occur on the bottom or in the few meters of water just above it, during the middle of the day. The reviewer has collected sexually mature specimens on several occasions in Cayuga Lake, N. Y. near midday at depths of 6 meters or more from the bottom. Immature specimens were frequently encountered at these depths.

In the section on Simulidae (page 647), the following statement is encountered, "Blackfly larvae are found in the shallows of streams where the current is especially swift." The reader is given the impression that this is the only place they occur. No mention is made of those which occur in roadside ditches, deep rivers, and slow streams.

These and other similar statements encountered throughout the book constitute a weakness which could have been avoided through the use of qualifying words with no loss of meaning.

The format is attractive and the binding and quality of paper is very good. Despite its large size and relatively high cost it will be indispensable as a text and reference for invertebrate zoologists. It surpasses in quality and in usefulness other existing books dealing with the freshwater invertebrates of this country.

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An English Text on Animal Ecology[1]

The book under review is a text designed to give a broad treatment of the subject matter of animal ecology for use, by and large, in the first year of university. The wealth of examples, which Dowdeswell uses to illustrate principles, are purposely drawn from the United Kingdom. For this reason the book is decidedly local in content and will appeal more to English rather than American students. The first four chapters cover such topics as the scope of ecology, paleoecology of the Pleistocene in Britain, distribution, movements and interrelationships (epizoites, commensals, parasites) among animals. The presentation here is lucid and informative, but exhibits many gaps. The discussion of populations mentions nothing of theoretical and experimental approaches to the phenomena of population growth and species interactions. Migration is lightly touched upon, but the colorful theories of homing, which would surely incite the imagination of a beginner, are left unmentioned. The principle of the food chain is developed and exemplified. Chapter II on animal distribution is well written and probably is the best in the book, though it suffers greatly from the lack of biogeographic treatment on a world-wide scale.

The second quartet of chapters covers the terrestrial, marine, estuarine and fresh water environments. These chapters abound with examples of ecological relationships, but they are defective in that the *oikos* of the animal is poorly outlined. Marine ecology, for example, is abruptly terminated at a depth of 100 fathoms. In the chapter on terrestrial ecology there is no mention of soils in relation to plant and animal succession, but instead there are sections on mimicry and territory that might better have been placed elsewhere, since they are not peculiar to the terrestrial environment. One is barely led to suspect the thermocline in the hydrosphere, and the name is not used. Diurnal migration of zooplankton is cursorily outlined and the problems of cyclomorphosis are overlooked.

The ninth and final chapter, entitled "Practical Animal Ecology" should not mislead the American reader for it is devoted to methods and apparati: construction and use of nets for collecting insects and plankton, dissolved oxygen measurement, thermistors, pH and so on. There is also a section on sampling and statistical significance of samples.

Dowdeswell's text appears to have two main defects. First of all it is devoid of many of the theoretical and quantitative formulations which the science of ecology has espoused. The second defect, perhaps justifiable, is the non-use of ecological jargon. Territory and succession are defined and used, community is used but not defined, and the reader is denied such pleasantries as the ecotone, biocoenosis, biome, geobiont and the like.

To be greatly commended is the use of generic and specific names throughout, even though the text is intended for students at an elementary level. There are no references in the body of the text, but there is a good bibliography along with a glossary of terms at the end. Dowdeswell has covered the vast and expanding field of animal ecology as well as any other text that has been designed for the elementary student. The book is well worth reading, and does not seem to be overly burdened with errors. While it has been designed for English students, the reviewer believes that it may serve as a useful reference in American ecology courses.

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[1] Dowdeswell, W. H. 1952. Animal Ecology xv + 207 pp., 45 figs., 16 plates. London: Methuen & Co., 12*s*. 6*p*.

Those of the Forest[1]

Many professional ecologists as well as other persons who enjoy nature will obtain pleasure and profit from reading Wallace Grange's "Those of the Forest." The book tells the story of the seasonal and annual changes that take place in a forest in northern Wisconsin. The action centers around an imaginary sequence of snowshoe hares, but involves ultimately many of the plants, vertebrates, and invertebrates of the forest community. While the action is imaginary, the writing is based on the field observations and reading of an experienced and completely honest field naturalist. The point of view throughout is ecological. The interdependence of the numerous

[1] Grange, Wallace Byron. 1953. Those of the Forest. Illustrated by Olaus J. Murie. iii + 314 pp. Babcock, Wisconsin: Flambeau Publishing Company. $4.75.

associated species is stressed. The writing is sympathetic, but not sentimental. It is recognized that each individual organism ultimately must die and that death from attack by herbivore or predator is no more unnatural and not necessarily more painful than death from cold, heat, drought, starvation, disease, or old age.

The picture given is of a considerable amount of repose in the lives of wild animals, alternating with usually shorter intervals of activity and of the frequent occurrence of satisfaction as opposed to rarer episodes of pain. Grange here is in pleasing contrast with some other writers about nature who depict wild animals as living in a nearly constant state of excitement and fear.

The book is interestingly written and is well printed on good paper. The sketches by Olaus J. Murie are, as always, excellent. It is highly recommended to all naturalists.

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Historical Aspects of Evolution[1]

The author of this work states in his introduction that a "certain amount of personal bias is bound to creep in." Unfortunately the bias does not creep in but rather runs in. The bias appears to have two facets, one religious and the other anti-Darwinian.

A summary impression of the book indicates that the author grudgingly accepts evolution as a working hypothesis and, having done so, proceeds to champion all the various dissenters from the Darwinian and Neo-Darwinian schools. Apparently it matters little to the author that theorists such as Lamarck, Lotsy, Willis, and Goldschmidt cannot be made bedfellows by any Procrustean device. It is sufficient that they are dissenters.

This negativism is accompanied by the use of prejudicial words, misquotations of eminent scientists and simple omission of pertinent historical facts. Further, the book redounds in poor logic and misunderstanding of evolutionary terms. There is practically no discussion of modern statistical theories of evolution developed by Wright, Fisher, and Haldane. The ecological side of evolutionary study is omitted almost completely. No research work done since 1940 is discussed. Selection of material for discussion from work produced prior to this time seems rather peculiar. Anderson's work on introgressive hybridization is not mentioned while Kammerer's results are detailed without so much as a word on the sad history of this biologist and his work.

One particularly startling aspect of this book is that the author should feel it necessary to attack implicitly the character of Charles Darwin. One quotation will illustrate this: (p. 117)—after a quotation from Samuel Butler which implies that Darwin reaped the rewards of the labor of E. Darwin, Lamarck, and Buffon—"Darwin did this so expertly that he persuaded people that he had produced a new theory of creation at a time when the old one was much the worse for wear." This quotation is also a good example of the use of prejudicial words by the author.

One gets the impression from the book that Sonneborn, Jennings, and Sumner had quite favorable attitudes toward Lamarckian theories. Jennings is misquoted (p. 252) while all three are quoted out of context. The book is rife with this sort of thing.

From the historical viewpoint this is a bad book. Darwin is criticized for lacking a theory of heredity which did not appear until long after his death. Early theories are criticized in the light of later knowledge while later theories are criticized on the basis of earlier erroneous concepts. Scientifically the book is no better. It is replete with errors of scientific fact and rather than being critical is simply negative. The reviewer suggests that students refer to other sources for information and critical analyses of theories of evolution.

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[1] Fothergill, Philip G. 1953. Historical Aspects of Organic Evolution. xvii + 427 pp. New York: Philosophical Library Inc. (Price not indicated.)

Dune and Downland Autecology and Ecosystems[1]

Sir Edward Salisbury, Director of Kew Gardens and Fulleton Professor of the Royal Institution, has integrated extensive research of his own and former students at University College in this comprehensive account of the flora, vegetation and habitats of the English chalk downs, limestone belts and sand dunes. The book is based on two courses of popular lectures, supplemented by several chapters of "biological notes" on morphological and ecological traits of important species.

The author's approach is hard to "type," since it spans the nineteenth century tradition of "natural history" and several current research trends. On the organization levels of individual and species, taxonomic and floristic comments are supplemented by intensive data on gross morphology and ecological life history, which in turn suggest problems in physiology. On the level of a "larger system," treatment of the vegetation complex includes the true naturalist's broad grasp of the significance of the whole landscape, and extends to detailed quantitative analysis of inter-relations between vegetation, substrate, microclimate and (in a few striking cases) animal populations, including man. Without using Tansley's term the author almost takes the all-inclusive *ecosystem* as his frame of reference, and analyses its structure and processes in some detail.

It is interesting to note how well his rambling (even quaint) style serves to develop complex ideas, quite free of the technical jargon and dogma of stereotyped approaches in the ecological literature. Although indispensable for attaining one stated objective of reaching "the general reader interested in the countryside," this policy benefits the scientist by defining the meaning of basic concepts instead of covering them up with ambiguous words. His interpretations of succession, for example, seem clear without benefit of Clementsian terminology or implications.

[1] Salisbury, Sir Edward. 1952. Downs and dunes: their plant life and its environment. 328 pp., 74 photographs, 93 line drawings and diagrams, 54 distribution maps. London, G. A. Bell and Sons, Ltd. 45*s*.

On a gross level he seems satisfied with physiognomy of dominant species as a basis for community delimitation without intensive phytosociological analyses. His critique (p. 26) that the use of constancy and exclusiveness of species to characterize plant communities is, "from the outset, doomed to have very limited value" is based partly on the assumption that many exclusive plants have low expected densities, and the proposition that this leads to a high probability of absence, or low constancy, due to chance alone. On the floristic level he seeks out cases of individual species whose restriction in distribution can apparently be interpreted in terms of physical, chemical or biological factors, noting that the same factor (e.g. soil warmth) may lead to a very "exclusive" distribution in one area (e.g. *Salvia pratensis* on English chalk) and a much less restricted pattern elsewhere (many other soils of continental Europe, where this species is not associated with a calcicole floristic element).

Turning first to the second half of the book, we find that it culminates the English contribution to the tradition of dune ecology which was started by Warming and Cowles. Because extreme habitat conditions so obviously limit the dune flora, fauna and biotic communities, on the one hand, and because organisms play a vital role in building dune landforms, stabilizing them and moderating the extreme habitat, on the other hand, sand dunes have particularly well illustrated the need for and possibilities of a scientific viewpoint encompassing such reciprocal inter-relations of organisms and environment. Such problems were beyond the scope of nineteenth century botanical and geographical traditions; the recognition of their importance and the establishment of a twentieth century tradition of ecology aiming at their fuller understanding seem to have been catalyzed by such classic dune studies, giving them a significance in the development of ecological thought beyond that of the sand dunes themselves.

Sir Edward suggests many interesting interpretations of his extensive quantitative data on the moisture regime, temperatures and soil composition of the dune habitat in terms of the morphological and physiological adaptations of dune species. For example, the water supply at depth is thought to be sufficient for the deeply rooted perennials throughout the year but to limit the distribution of shallow rooted species, except for winter annuals which complete their life cycle before summer dry spells. Although unfavorably high surface temperatures must be tolerated by all plants surviving the summer, favorable warming of soil surface and plant parts above the low air temperatures of winter and spring presumably help these winter annuals to complete their life cycle before the very high summer temperatures are encountered. Condensation of moisture from the damp air directly onto the chilled dune surface at night, and movement from the warmed surface soils to the cooler soils beneath during the day is suggested as a mechanism for replenishing the limited moisture that the dune sand can hold. The apparent demonstration of diurnal moisture fluctuations at great depths where free energy gradients and vapor conduction should be relatively small poses the question of whether plants might be serving as agents absorbing moisture from the air, conducting and exhuding it to the soil—suggesting still another way in which the vegetation and habitat might be interacting.

Typical dune successions, from dune-building grasses (most notably *Ammophila arenaria*) and a few other species tolerant of shifting substrate and environmental extremes to vegetation consisting of a larger, less specialized flora in the moderated habitats of older dunes, have their counterparts elsewhere, though there are many interesting details peculiar to the English dunes. The dramatic demonstration of succession, by rather complete relative age sequences available on series of dune ridges, constitutes another reason why dunes have received special attention in the history of ecology. Sir Edward has gone further than is usually possible by providing an absolute age calibration (from annual rings of *Salix repens,* from old maps, etc.) for the Southport and Blackeny Point dunes, which are among the relatively few case studies (besides early old fields) for which we have chronological data on the rates of succession. His work is particularly interesting because of the large number of analyses showing the accompanying changes in the soil development, from calcareous alkaline sand to acid organic soil having higher moisture capacity and lower aeration. Whereas the calcareous southwestern English dunes develop shrubs of privet and elder, followed by English oak and hazel if sufficiently undisturbed by man and rabbits, the less calcareous dunes of northern Britain develop a very persistent dune heath, with slight indication of succession toward Scotch pine, which is usually accelerated by man's forest plantations. However, these differences in parent material are confounded with differences in rainfall and presumably other climatic variables which are difficult to evaluate.

Sir Edward emphasizes the rather high calcium content which prevails in almost all beach sands and hence young dunes (because of shell fragments as well as limestone sand) and the supposedly calcicole floristic element of the young dunes and of the moist interdune "slacks" which receive the lime leached from the dune soils. This floristic element is one of the few things which the dunes, chalk downs and limestone areas seem to have in common. However, the treatment of soil development and the geochemical cycle of calcium, as they affect and are affected by both plants and animals, is a theme which is repeated in each section of the book, with variations according to the different circumstances of each region.

The chalk, for example, consists of 95% to over 99% finely divided calcium carbonate, but rainwater, carbonated by plant roots, tends to leach away about a thousand kilograms per hectare per year (a little less than a thousand pounds per acre per year), eventually leaving a surface soil concentration of insoluble residue. Organic decomposition in this soil may lower the surface pH from around 8 to below 5 (rarely) on level hill crests, permitting even calcifuge species such as heather to grow on local patches. One process counteracting this tendency is erosional removal of this residue, most completely on the steeper slopes, which therefore maintain greatest lime influence and the most characteristic calcicole flora. Another process renewing the carbonate influence is the return of calcareous subsoil fragments to the surface by rodents, earthworms and ants. Plants also participate in the calcium cycle by returing lime to the surface in their litter.

The most calcareous soils show evidence of deficiency in available phosphorus, iron, manganese and boron, which might be limiting factors excluding certain species from the chalk flora. However, *Azotobacter* and nitrification processes as well as many of the higher plants are thought to be favored by high calcium content directly, and also indirectly through greater molybdenum availability. Pot experiments suggest that the calcium ions of chalk stimulate plant roots to more extensive growth, and the typical stratification of a moderately acid surface soil over a more alkaline subsoil apparently provides different optimal conditions for the absorption of different nutrients by different parts of the single root system.

Physical effects of the substrate are also believed to be important in selecting some species of the chalk flora,

particularly those characteristic of a southern continental climate. The high porosity of chalk leads to good aeration, and this to a warmth of surface soils, especially on sunny south slopes. Although drying out of a surface soil may be a serious danger for shallow rooted species, as in the dunes, there is normally a fairly permanent supply of available water below half a meter's depth.

Sir Edward believes that vegetation has responded sensitively to past climatic changes. "Neolithic man's advent in these islands was contemporaneous with the comparatively warm and moist conditions that obtained towards the close of the 'Atlantic period' during which the forests of Oak, Alder and Lime reached their maximum development. With the subsequent climatic fluctuations to the warmer and drier sub-boreal conditions of the Bronze Age the circumstances had become more favorable to species associated with a continental climate and it was about this time, some 3,000 years ago that we first have evidence of the Beech tree in Britain, possibly then, even more than now, confined to chalk by reason of the intolerance of this tree for ill-drained soils."

On shallow chalk soils beech now dominates the forests almost completely, constituting several age classes representing occasional "mast years." Except along margins or in openings, its intense shade and shallow root system restrict the shrub layer to a sparse growth of a few species, such as yew. Like the early vernal wildflowers, these must assimilate most of the year's food before the expansion of the dense beech foliage reduces light from between 17% and 70% to between .4% and 4% of full sunlight. Oak accompanies beech on deeper soils, while a chalk ecotype of ash is limited to former canopy openings or edges or occasional wet spots where beech cannot compete so severely.

"The clearance of woodland scrub, which Neolithic man began, has probably continued almost without interruption during the past four millenia and the trees and shrubs that man removed by fire and the axe have been prevented from returning by the browsing of flocks of sheep [particularly from the twelfth century through the nineteenth] and, since Roman times, by the rabbits also. Because grasses are pre-eminently tolerant of repeated mowing, whether by machine or ruminant, the preponderance of such plants [particularly drought resistant types such as *Festuca ovina, F. rubra,* and *Koelaria gracilis* (or *cristata*)] is natural." Grazing pressure, like mowing, favors a large number of low forbs, particularly rozettes, at the expense of the more limited number of tall species. Comparing the same degree of grazing, the steeper slopes with shallower soils maintain more open vegetation and niches for species of poor competitive ability.

Secondary successions from pasture scrublands and cut forests, as well as from unrewarding old fields abandoned after temporary wartime cultivation, provides interesting parallels in events and formulation with those of American ecology. The biotic factors of seed source and dispersing agents and seedling browsing are fully appreciated. Unless accelerated by exclosures, succession may be a very slow process except around the expanding protective periphery of thickets, which typically start in favorable niches in moist valleys and creep upslope.

Although the limestones share a calcicole floristic element with the chalk, their higher insoluble residue content (averaging 11% and in some cases exceeding 50%) leads to deeper and generally moister soils. Greater moisture and lower temperature are thought to be related to the absence of the continental element of the limestone flora. The abundance of ash as the forest dominant is attributed to its greater tolerance of high water content (presumably poor aeration), shown by its occurrence on marshes, both calcareous and non-calcareous. The light foliage (often 17%), persisting only from about May 10 to October 16 (as compared with April 25 to November 22 for beech and intermediate dates for oak) permits abundant shrub and herbaceous growth.

Typographical errors seem to be too minor to list. The fine photographs of individual plants and landscapes serve as a pleasing background almost independent of the text. The author's many neat line drawings are very effective in illustrating particular points of discussion.

Although the four page bibliography shows that much of the original research was done two to four decades ago, it is a credit that it compares as favorably as it does with current standards. The many questions left incompletely answered are to be expected in any forward-looking research, and their eventual solution will presumably fill out and enhance, rather than detract from, the broad picture which Sir Edward has painted so artistically.

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